

**The Eastern Bering Sea:
Three Decades of Change**

George L. Hunt, Jr.¹, Phyllis Stabeno², Gary Walters³, Elizabeth Sinclair⁴
Richard D. Brodeur⁵, Jeffery M. Napp³, Nicholas A. Bond⁶

- ¹. Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697-2525. e-mail: glhunt@uci.edu, Phone: 949-824-6322
- ². Pacific Marine Environmental Laboratory/NOAA, 7600 Sand Point Way NE, Seattle, WA 98115. E-mail: stabeno@pmel.noaa.gov, Phone: 206-526-6453
- ³. National Marine Fisheries Service/NOAA, 7600 Sand Point Way NE, Seattle, WA 98115. Email: jeff.napp@noaa.gov, gary.walters@noaa.gov; Phones: Napp- 206-526-4148; Walters- 206-526-4143 .
- ⁴. National Marine Mammal Laboratory/NOAA, 7600 Sand Point Way NE, Seattle WA 98115. Email: Beth.Sinclair@noaa.gov . Phone: 206-526-6466
- ⁵. National Marine Fisheries Service/NOAA, Hatfield Marine Science Center, Newport OR, 97365-5296. Email: Rick.Brodeur@noaa.gov , Phone: 541-867-0336
- ⁶. Joint Institute for the Study of Atmosphere and Oceans, University of Washington, Seattle, WA 98195-4235 E-mail: bond@pmel.noaa.gov; Phone: 206-526-6459.

ABSTRACT:

In this paper, we review and offer new data on three decades of physical and biological records in the eastern Bering Sea including patterns of ice coverage, wind mixing, sea surface temperature, timing of blooms, zooplankton productivity, fish biomass and distribution, and marine bird and mammal population trends. In examining these patterns, we show that the combination of time series and process studies combined predict future responses of the eastern Bering Sea to climate change.

During the past three decades, major variations in the physical and biological characteristics of the eastern Bering Sea have occurred at annual to decadal scales. During this period, two and possibly three regime shifts have been identified. In the late 1990s, inter-annual variations encompassed nearly the full range of extreme conditions documented in the past 30 years. The spatial scales over which variations occurred have differed depending on the index of change measured. At the largest spatial scales, atmospheric anomalies have influenced the entire eastern northern North Pacific Ocean and Bering Sea, yet when examined at the smaller scale of subregions within the eastern Bering Sea shelf, it is organism responses that have the most demonstrable differences between regions.

Since the mid-1990s, the Southeastern Bering Sea Carrying Capacity (SEBSCC) and the Inner Front (IFP) programs have conducted process studies and developed time-series for physical and biological components of the southeastern Bering Sea shelf. Evidence now supports the hypothesis that the timing and duration of primary production is controlled by the timing of ice retreat and the cessation of winter winds, with late ice retreat (April-May) leading to an early, ice-associated bloom. Zooplankton populations are probably not closely coupled to primary production, but are sensitive to water temperature, which is also related to the timing of ice retreat and cessation of winter winds. Long-term data suggest little change in overall zooplankton biomass, although copepods were at elevated densities in 1997 compared to 1981.

Since the late 1970s, the biomass of large predatory fish and gelatinous macrozooplankton has increased markedly, and the biomass of forage fishes, including age-1 walleye pollock, has fallen, particularly over the southern portion of the shelf. Picivorous marine birds and northern fur seals at the Pribilof Islands have declined, most probably in response to a diminished prey base, but populations of both are healthy in the western Aleutians, and, in the case of marine birds, along the west coast of Alaska. We suggest that the spatial heterogeneity of apex predator responses reflects dependence on different, localized food webs.

We propose a new hypothesis, the Oscillating Control Hypothesis, in which the control of pelagic ecosystem function alternates between a bottom-up control in cold regimes and top-down control in warm regimes. In cold regimes, low water temperatures limit the abundance of zooplankton and fish populations will be limited by the availability of zooplankton. In contrast, in warm regimes abundant predatory fishes control forage fishes and limit their ability to crop zooplankton. Over the course of a warm regime, populations of large predatory fishes should decline when they exert severe predation pressure on their young. When there is a shift from a cold regime to a warm regime, zooplankton biomass increases rapidly and forage fish respond with strong year-classes and high survival under reduced predation pressure. This hypothesis, if correct, suggests that the ability of large predatory fish populations to sustain fishing pressure may vary between regimes. Time series necessary to test the predictions of this hypothesis are lacking.

Introduction

In the past three decades, major changes have occurred in the marine ecosystem of the eastern Bering Sea and the nearby Arctic and Subarctic (Schumacher *et al.*, In Press). Evidence of warming, including melt-back of glaciers, thinning of the Arctic ice cover (Waddams, 1995), and warming and or melting of permafrost (Osterkamp, 1994), is pervasive. In the southeastern Bering Sea, major changes in stocks of salmon, crab, and groundfishes have caused significant economic impacts (NRC, 1996; Schumacher *et al.*, In Press). Likewise, changes in some populations of marine birds and mammals have focused attention on the resilience of the ecosystem to changes in harvested fish populations. The closure of critical feeding habitat of Steller sea lions (*Eumetopus jubatus*) to all trawling for groundfish is a result of the concern about the potential relationships between events that are taking place (United States District Court for the Western District of Washington, 2000). What is needed now is a better understanding of the causal relationships between climate, production and the population dynamics of upper trophic-level organisms (e.g., Livingston and Tjelmeland, 2000). This information is vital for understanding the limits of what fisheries management can achieve, and for understanding the relative impacts of climate variability and marine harvest in structuring the Bering Sea ecosystem (Witherell *et al.*, 2000).

Changes in the species composition and functional linkages of marine ecosystems can be forced by both natural and anthropogenic factors. Natural factors in the Bering Sea include climate-induced storm activity, sea-ice cover, sea temperatures and shifts in the location or strength of current systems. Direct anthropogenic factors include release of pollutants, removal by commercial and non-commercial fisheries, and habitat disturbance. Both natural and anthropogenic factors can act as bottom-up regulators by affecting the amount of primary production, and thereby the abundance of prey available to higher trophic levels. By competing for prey, they can also induce top-down regulation by affecting the fate of production or by altering the abundance or distribution of

predators available to crop prey. We examine time series of physical and biological data from the eastern Bering Sea shelf for evidence of the effects of climate or weather on bottom up and top down regulation of the ecosystem. These time series provide a context for the process studies conducted in the NOAA-sponsored Southeast Bering Sea Carrying Capacity (SEBSCC) program and the NSF-sponsored Inner Front Project (IFP) that constitute the majority of the work reported in this volume.

In the early 1990s, hypotheses were developed to explain changes in the populations of some top predators in the southeastern Bering Sea, such as the Steller sea lion and the red-legged kittiwake (*Rissa tridactyla*) (e.g., Anonymous, 1993). More recently, the focus broadened to explain changes in the structure of the marine ecosystem (e.g., NRC, 1996; Merrick, 1997; Sugimoto and Tadokoro, 1998). Early studies identified the lack of forage fishes, particularly those species with high fat content (e.g., capelin, *Mallotus villosus*, and lantern fish, *Myctophidae*), as being a factor in the declines of seabirds and pinnipeds (Sinclair, 1988; Anonymous, 1993; Sinclair et al., 1994, 1996; Decker et al., 1996; Hunt et al., 1996b; Merrick et al., 1997). Initially, declines in forage fish abundance were hypothesized to result from predation by walleye pollock (*Theragra chalcogramma*) (Springer, 1992), and later from climate change (Piatt and Anderson, 1996; Springer, 1998).

Merrick (1997) reviewed alternative hypotheses concerning the lack of prey necessary to support pinnipeds and marine birds. The Oceanic Regime Shift Hypothesis (ORSH) ascribes changes in fish populations to the direct effects of ocean warming. The Commercial Fisheries Hypothesis (CFH) and the Trophic Cascade Hypothesis (TCH) emphasize the importance of the anthropogenic removal of stocks from the eastern Bering Sea. According to the CFH, commercial fisheries may have depleted the abundance of mature fish in the vicinity of rookeries of Steller sea lions and northern fur seals (*Callorhinus ursinus*). Alternatively, according to the TCH, the removal of large whales, fur

seals, Pacific herring (*Clupea pallasii*) and Pacific ocean perch (*Sebastes alutus*) may have initiated a trophic cascade (Merrick, 1997). Their absence from the ecosystem then could have allowed juvenile pollock to exploit the zooplankton formerly taken by these species, which resulted in a rapid expansion in the biomass of pollock and other groundfish. In this paper, we present time series germane to evaluating the ORSH. We focus on bottom-up mechanisms and top-down relationships evident in the time-series and useful as a context in which to place the work presented in this volume.

Climate, and in a more immediate sense weather, determines sea surface temperature, surface currents, and mixing. Several indices of wintertime atmospheric and oceanic conditions are available. These indices, in conjunction with other parameters of ecosystems, have been used to identify abrupt shifts in climatic forcing and ecosystem response at decadal time scales (e.g., Trenberth and Hurrell, 1995; Mantua et al., 1997; Francis et al., 1998; Hollowed et al., 1998; Springer, 1998; Hare and Mantua, 2000). Two of these so-called regime shifts have been identified in the past thirty years. One followed the winter of 1976-1977, in which the Pacific Decadal Oscillation (PDO) and the Arctic Oscillation (AO) shifted (Fig. 2). A second shift, indicated by just the AO, occurred after the winter of 1988-1989 (Ebbesmeyer et al., 1991; Hare and Francis, 1995; Sugimoto and Tadokoro, 1998; Beamish et al., 1999; Brodeur et al., 1999a; Hare and Mantua, 2000). The PDO has been negative since June 1998 (the end of the last El Niño), and a third regime shift may have occurred, but the evidence for this shift is still accumulating (Stabeno et al., 2001). The climate of the Bering Sea, at the southern extent of the Arctic region, shifts with respect to changes in both the AO and the PDO (Overland et al., 1999).

Identification of the regime shifts has depended not only on physical indices, but also on the responses of higher-trophic-level organisms, such as jellyfish and salmon, which offer the most obvious reflection of change in marine ecosystems. However, correlations between an atmospheric index and seabird

or marine mammal populations leaves unidentified the mechanisms by which climate and weather force physical and biological processes. This information is important if we are to predict future ecosystem responses.

In this paper we examine temporal and spatial variability in physical and biological aspects of the southeastern Bering Sea ecosystem. Of interest are the roles of physical parameters and processes in determining the timing, magnitude and fate of primary production. We also draw upon time series of the populations and diets of upper trophic level organisms such as jellyfish, fish, seabirds and marine mammals. Examinations of their populations, distributions and diets provide insights into how climate has affected the structure and function of this marine ecosystem.

STUDY AREA

The southeastern Bering Sea shelf is a broad, shallow region, up to 500 km wide (Fig. 1). Shelf waters are differentiated by hydrographic and current domains associated with characteristic bottom depth ranges (Kinder and Schumacher, 1981; Coachman, 1986; Schumacher and Stabeno, 1998; Stabeno et al., 2001). The coastal domain (depth < 50 m) typically is either weakly stratified or well mixed as a result of a combination of tidal and wind mixing. In the middle shelf domain (depth between 50 and 100 m), mixing energy is not sufficient to stir the entire water column in the presence of a positive buoyancy flux during summer. A strongly stratified two-layered water column results, with a wind-mixed surface layer (15 to 40m), and a tidally-mixed lower layer (~ 40 m). The outer shelf domain (depth between 100 and 180 m) has a three-layered structure. Transition zones (middle transition and shelf break front) separate the middle shelf from the outer shelf, and outer shelf from the slope waters, respectively (Coachman, 1986; Schumacher and Stabeno, 1998; Stabeno et al., 1999). A structural front <10 km wide separates the middle and coastal domains

(Schumacher et al., 1979). This feature is evident along the entire southeastern shelf to north of Nunivak Island. A similar feature exists around the Pribilof Islands (Kinder et al., 1983). A lack of advection and minimal horizontal fluxes of heat and salt across the structural front are suggested by observations (Coachman, 1986; Kachel et al., this volume).

In the middle domain, the upper mixed layer readily absorbs heat in spring. The estimated rate of heating is 2 to 2.5 °C month⁻¹ in the upper layer and ~ 0.5 °C month⁻¹ in the lower layer, compared to ~ 1.5 °C month⁻¹ in coastal waters (Coachman 1986). During late July, the temperature difference between the upper and lower layers can be greater than 8 °C. During summer, changes in temperature dominate changes in salinity and hence are critical to the physical dynamics.

Circulation in the coastal domain is dominated by flow (1 - 6 cm s⁻¹) northeastward along the Alaska Peninsula, counter-clockwise around Bristol Bay, and then northwestward past Nunivak Island (Fig. 1). This flow is concentrated in the vicinity of the 50 m isobath (Schumacher et al., 1979). The source of this flow is mainly the Alaska Coastal Current that enters the Bering Sea through Unimak Pass reinforced by freshwater addition (Schumacher and Kinder, 1983; Schumacher and Moen, 1983; Stabeno et al., this volume). Flow, either through Unimak Pass or onto the shelf from the adjacent slope, produces elevated nutrient concentrations in the vicinity of the pass (Schumacher and Stabeno, 1998; Stabeno et al., this volume).

High rates of primary production have been reported throughout the Bering Sea, especially on the northern shelf and along the shelf edge (Springer et al., 1996). Over the southeastern Bering Sea shelf, primary production varies between domains, with the greatest production occurring in the outer and middle domains (Iverson et al. 1979a; Walsh and McRoy, 1986; Springer et al., 1996). Abundant nutrients and incident radiation support high primary production rates

during the spring bloom. However, nutrients become limiting within a short period over most of the shelf because of the establishment of a strong pycnocline (Whitledge et al., 1986). In the middle shelf, a chlorophyll maximum persists in the pycnocline into the fall (Iverson et al., 1979a) and this observation implies that production continues in this subsurface layer, as is the case on other continental shelves (Holligan et al., 1984; Richardson and Christofferson, 1991). Occasional mixing events from summer storms provide the only general enrichment of surface waters on the middle and outer shelf (Whitledge et al., 1986; Sambrotto et al., 1986). In comparison to the general depletion of nutrients in surface waters, the frontal regions (outer, middle and inner) contain relatively large surface concentrations of both nutrients and phytoplankton throughout late spring and summer (Iverson et al., 1979a,b).

RESULTS

Weather, Physical Properties and Production

Sea-ice cover and wind-forced mixing are important determinants of the timing and duration of spring primary production, and influence the production of prey for larval fish (Napp et al., 2000). Sea-ice is formed in polynyas present in the lee of islands and coastal regions (Niebauer et al., 1999). This ice tends to be blown south by the prevailing winds and melts at its southern edge, cooling the sea water (Pease, 1980; Niebauer et al., 1999). The maximum southerly extent of the sea-ice varies greatly inter-annually (Stabenho et al., 2001), but it is the timing of ice-retreat in spring that may have the more critical effect on the ecosystem.

To examine the effects of sea ice on production in the eastern Bering Sea, we obtained the position of the ice edge from the National Ice Center, the Fleet Numerical Meteorology and Oceanography Detachment and the National Climatic Data Center. This data set contained data from 1972-1994. For the

years since 1994, we used the Alaska Regional Ice Charts, obtained as maps from the Anchorage Forecast Office of the National Weather Service. These maps were digitized. The concentrations in each 1° block were obtained by averaging the concentration in each grid cell.

As expected, variability in sea-ice coverage was greater at the southernmost extent of the ice field than in regions farther north (Fig. 3). Between 59° and 60° N, there were no years when ice was largely absent, nor does there appear to be a trend in the timing of ice retreat. In contrast, between 57° and 58° N, there was an increase in the number of periods with little or no ice after 1976. In addition, there was a trend toward later arrival and earlier departure of ice, particularly after 1989. Strong inter-annual variability in ice concentrations makes the identification of decadal-scale variability difficult in this short time series. However, it can be said that the pattern of ice coverage has changed since the 1970s (Fig. 4). Then, the maximum extent of the zone in which ice was present annually for >2 weeks extended farther south and west than was true in the 1980s or the 1990s. Additionally, in the 1980s and 1990s, the zone where ice lasted for at least two weeks withdrew northeast along the Alaska Peninsula until the north side of the Peninsula was ice-free all winter. The source of the heat to melt ice along the Peninsula is not known. It could be from warm water (~ 3... C) advected into the Bering Sea from the Gulf of Alaska via Unimak Pass, or from water that flowed from the basin up Bering Canyon (Stabeno et al., 2001). Regardless of the heat source, the increase of open water north of the Alaska Peninsula suggests that there has been an increase in the flow of water to the northeast across the shelf over the last two decades.

Additional support for cross-shelf flow comes from observations of biota that act as passive drifters in surface waters. In 1998 and 1999, oceanic copepods (*Neocalanus* spp. and *Eucalanus*) were more abundant over the middle shelf and along the inner front than expected (Hunt et al., 1999; Napp and Hunt, 2001). Additionally, in both 1998 and 1999, floating pieces of bull kelp

(*Nereocystis luetkeana*), a macro-alga that grows sub-tidally along the west coast north and west to Unalaska Island, but not in the Bering Sea (Scagel et al., 1986), were observed throughout the middle domain (G. Hunt, unpublished data). Although Russian scientists recorded oceanic species farther onto the southeastern shelf in warm years (Coyle et al., 1996), temperatures over the shelf were average in 1998 (12... C) and below average in 1999 (< 9... C). The role of cross-shelf advection requires further investigation.

The wind field has also changed dramatically over the past decades (Fig. 5). From the 1960s through the mid-1970s, strong winds were recorded at St. Paul Is., Pribilof Islands, from late September through late April. Since about 1977, however, the period of summer calm has increased from about three months to five months, with low to moderate winds predominating from April through October. Winter storms are now mostly over by April, as opposed to extending into May or even June, as was previously the case.

The changes in the timing of ice melt in the spring and the shift from the strong winter winds to the relatively light winds of summer have important implications for the timing and duration of primary production (Fig. 6). When ice melt occurs in February or early March, as was the case in 1998, there is insufficient light to support a bloom, and the spring bloom is delayed until late May or June, when thermal stratification stabilizes the water column (Stabeno et al., 2001). If ice melt occurs in April or May, the water column is stabilized by the freshening of the surface layer, and an early, ice-associated bloom may begin while ice is still present (e.g., 1995, 1997). Strong winds at the time of ice melt can delay the bloom, as may have happened in 1975. However, lack of data precluded detection of an early bloom in that year, had one occurred.

Temperature and the Fate of Production

McRoy and Walsh (1986) hypothesized that the fate of production in the southeastern Bering Sea is influenced by water temperature since phytoplankton

growth is less sensitive to water temperature than is zooplankton growth (see also Townsend et al., 1994). Thus, when water temperatures are depressed by sea ice and northerly winter winds, the spring phytoplankton bloom will be less vulnerable to control by zooplankton grazing because zooplankton reproduction and population growth will be retarded. Therefore much of the phytoplankton will sink ungrazed to the bottom to support a rich benthic food web (e.g. clams, crabs and flatfish; Livingston et al., 1999). In contrast, when winter/spring water temperatures are relatively warm, zooplankton reproduction and population growth occur at higher rates, and a larger fraction of spring primary production will be consumed by zooplankton, thereby supporting a pelagic food web (e.g., mid-water fishes).

Although the temperature of the water column in spring is crucial to elements of the marine ecosystem, most effort has focused on documenting winter conditions over the Bering Sea shelf (e.g., Niebauer et al., 1999). We assessed long-term variation in springtime through early summer sea surface temperature (SST) using the Global Ice and SST data set produced by the United Kingdom Meteorological Office (Parker et al., 1993). To do so, we extracted a time series for 56° N, 165° W, a location representative of the middle-shelf domain. Our objective was to document how the spring and summer warming of SST in the recent past compares with earlier periods. To this end, we plotted three-year running means of SST at semi-monthly intervals from mid-April through the end of July (Fig. 7). We found that over the last three decades, there has been a tendency toward warmer summertime SST, and also a reduction of mixing across the pycnocline that could influence the amount of summertime primary production.

On a decadal scale, there was a period of unusually cold springtime temperatures from the late-1960s to the mid-1970s (e.g., Fig. 7, 15 April time-series), and a period of unusually warm temperatures from 1977 through the mid-1980s. Early summer SSTs also show the cold dip in the 1960s to 1970s, but

since 1977, there has been a warming trend that has led to $\sim 1^{\circ}\text{C}$ increase in SST (e.g., Fig 7, 15 June to 15 July time-series). The transition coincided with the "regime shift" in the climate of the entire North Pacific (e.g., Mantua *et al.*, 1997). Since the early-spring surface temperatures reflect water column temperatures in well-mixed water, the diverging trends in sea-surface temperature between spring and summer suggest a trend toward increasing temperature stratification.

The effects of anomalies in wintertime forcing and oceanic response can carry over into the following summer, as is apparent for the early to middle 1970s. There is also a suggestion of a long-term trend towards warmer SST during the middle of summer. The relatively warm mid-summer SSTs observed in the late 1990s can be attributed largely to anomalous warming around the first of June, as compared with most of the previous record. Bond and Adams (this volume) show that this warming has been caused by a combination of enhanced solar heating due to less cloud cover in May, June and July, and diminished evaporative cooling due to weaker winds. The weaker winds have also tended to reduce the mixing across the thermocline, and hence the entrainment of cooler, nutrient-rich water from below the upper mixed layer.

Zooplankton Populations

Evidence for change in zooplankton populations varies according to species and location. Early analyses of the long-term zooplankton data set from the Hokkaido University summer cruises suggested decreases in wet weight of all zooplankton (excluding jellyfish) (Sugimoto and Tadokoro, 1998). When this time series was plotted using only data from regions of the shelf that were repeatedly sampled by the Hokkaido University summer cruises, displacement volumes of zooplankton show a slight, though not statistically significant, decline in biomass between 1977 and the 1990s in the inner, middle and outer shelf domains (Fig. 8). In contrast, by-catches of large jellyfish in the National Marine Fisheries Service (NMFS) bottom trawl surveys show major increases over the

shelf (Fig. 9) (Brodeur et al., 1999a, ms), particularly since 1990. Increases in jellyfish biomass originated in the south and spread northward across the shelf.

Stockwell et al. (2001) found a significant increase in the biomass of neritic copepods (*Calanus marshallae*, *Pseudocalanus* spp., *Acartia* spp.) in 1997 when compared to samples collected in 1981, but the lack of a time series precludes determination of when these changes occurred. In contrast, there was no statistically significant change in the biomass of adult and juvenile euphausiids (*Thysanoessa raschii*) over the shelf between samples taken in 1980/81 and those taken in 1997/98 (Stockwell et al., 2001; Coyle and Pinchuk, this volume). With the exception of the sampling conducted by Hokkaido University, we lack the necessary time series to detect long-term trends in zooplankton populations.

Changes in Fish Populations

To examine changes in fish populations over the eastern Bering Sea shelf, we used the results of the NMFS bottom trawl surveys. These have been conducted with similar methods, over the same region and at the same time of year, for longer than any other survey of fish on the shelf. These surveys sample demersal populations well, but do not provide a quantitative sample of mid-water organisms. For instance, age-2 and age-3 pollock are in the mid-water, and are under-sampled, as are age-1 pollock. Nevertheless, this survey provides the best time series available for examining trends in the fish populations of the shelf.

Fish populations in the waters of the southeastern Bering Sea shelf have changed in both distribution and abundance since the mid-1970s. In particular, based on the results of NMFS bottom trawl surveys, the biomass of large predatory fish has increased, and while the bycatch of forage fishes, critical components of the prey of these large fish as well as of picivorous birds and pinnipeds, has declined. There also appears to be a generally northward shift in the distribution of fish biomass.

Adult walleye pollock are large predatory fish that make up the bulk of the gadids present on the shelf. Across the shelf, populations of both gadids (pollock, and Pacific cod, *Gadus macrocephalus*) and flatfish (arrowtooth flounder, *Atheresthes stomias*; northern rock sole, *Lepidopsetta polyxystra n. sp.*, Orr and Matarese, 2000) increased in the late 1970s to early 1980s and then stabilized through the rest of the 1980s (Fig. 10) (unpubl. NMFS bottom trawl data). Declines in gadid populations began about 1993, and flatfish populations appear to have begun to decline as of 1996 or 1998. Despite recent declines, for both gadids and flatfish, the biomass present in 1999 was more than twice the biomass present in 1975.

The pattern of distribution of age-2 and older pollock (age-2-plus) has changed since 1975, when the highest densities of pollock biomass were over the southern portion of the shelf, in the South Outer Shelf (42% of biomass) and South Middle Shelf (22% of pollock biomass) strata (Fig. 11). By the late 1990s, densities had declined over most of the southern portions of the shelf. The biomass of age-2-plus pollock apparently remained greatest in the North Outer Shelf and North Middle Shelf. These changes resulted in a major northward shift in the distribution of pollock biomass, with 81% in the North Outer Shelf and North Middle Shelf strata in 1999 as compared to 31% in 1975 (unpubl. NMFS bottom trawl data).

The timing of peak densities of age-2-plus pollock differed between strata. The South Outer, South Middle Shelf, North Middle Shelf and Inshore strata all showed biomass peaks in 1983 or 1984 resulting from the maturation of fish in the 1978 year-class. Biomass peaks between 1988 and 1990 in the North Outer, North Middle and Unimak strata again reflected the impacts of later year-classes. A set of peaks was also apparent in the southern portion of the shelf between 1993 and 1996, depending on the stratum. Some of the short-term variability may reflect changes in the vertical distribution of fish, and thus their vulnerability

to bottom trawls, whereas the longer-term patterns support the hypothesis that the fish have shifted to the north. The abrupt declines in biomass in many of the strata since 1996, and the overall decline in pollock biomass since 1995, may indicate that pollock have shifted their distribution northward, outside of the survey area. Alternatively, populations may be declining, possibly because of the decrease in forage fishes on which adult pollock and other predatory fish depend.

Arrowtooth flounder also showed an initial increase in density over the southern shelf, followed by increases in the north (Fig. 12). Peak densities were measured for most strata between 1992 and 1996, with all strata, except possibly the Southern Outer Shelf, showing strong declines in density subsequent to 1997. Densities of northern rock sole were initially highest near Unimak Pass, and then increased in coastal waters eastward and then northward across the shelf (Fig. 13). Northern rock sole densities were still increasing along the southeast shelf and peninsula in 1999, whereas elsewhere, peak densities occurred earlier in the decade. In the late 1990s, northern rock sole biomass was particularly great along the Alaska Peninsula and in the Inshore strata.

Forage fish, dominated by age-1 pollock, show great interannual variation as a function of pollock year-class strength (Fig. 10, Fig. 14) (unpubl. NMFS bottom trawl data). In virtually every stratum, the densities of age-1 pollock were highest in either 1976 or 1979, and at or near their lowest point in 1998-1999 (Fig. 14). In all strata, as age-2-plus pollock increased in biomass between 1975 and 1984, age-1 pollock decreased. However, in the 1990s, as age-2-plus pollock decreased in biomass, there was little indication of an increase in the biomass of age-1 pollock in any of the strata. Moderate to strong year classes since the very strong 1978 year-class have done little to elevate the densities of age-1 pollock other than in the North Outer Shelf stratum. Age-1 pollock have fallen to particularly low densities across the southern shelf. Since the early 1980s, there have been few age-1 pollock available to sustain marine birds or mammals near the Pribilof Islands, along the South Outer Shelf, or in the vicinity

of Unimak Pass. In two strata, other species provide the major component of forage fish (e.g., South Outer Shelf stratum, eulachon, *Thaleichthys pacificus*; Inshore stratum, herring, and capelin).

Capelin is a forage fish species that prefers cold water within a narrow temperature range (Methven and Piatt, 1991). In the eastern Bering Sea, Russian trawl surveys between 1969 and 1978 encountered capelin in water with bottom temperatures of — 1.7° to + 1.5... C (Naumenko, 1996b). During this period, large concentrations of capelin occurred near the Pribilof Islands in April and May and in late fall and early winter at depths of 60 m and bottom water temperatures of —1.8° to 2.0° C. In summer, capelin move inshore to spawn along the western Alaska coast from Togiak Bay to Norton Sound. Fish not taking part in spawning inhabit the seaward part of the shelf (Pahlke, 1985, in Naumenko, 1996b) and would presumably have been available to marine birds and pinnipeds breeding on the Pribilof Islands. However, in the late 1980s, capelin were well north of the Pribilof Islands (Brodeur et al. 1999b).

The summertime biomass of capelin around the Pribilof Islands declined in the mid- to late-1970s (Hunt et al., 1996b; Naumenko, 1996b). The biomass of pollock on the shelf rose from 2 million tons to about 10 million tons between 1965 and 1972 (Merrick, 1997). After this rise, pollock biomass declined to about 6 million tons in 1975, and stayed at this level until 1980, when the biomass rose rapidly to almost 15 million tons. Thus, the capelin decline occurred between 3 and 6 years after the pollock population had declined from its initial surge, and 3 to 5 years before its second surge. It seems likely that the disappearance of capelin from the Pribilof Islands region was because of increasing sea temperatures, rather than because of predation by pollock. The failure of capelin to return in subsequent years with low water temperatures may reflect competition or predation pressure from pollock, but there is no evidence available to support this conjecture.

In summary, the biomass of large predatory fish, in particular walleye pollock, increased rapidly after the shift from the cold years of the early 1970s to the warm years post-1976. The surge was fueled by the immense year-class of pollock in 1978. Subsequently, forage fish biomass declined; capelin apparently shifted their distribution northward in response to warming water temperatures, and, in the mid-1980s, the biomass of age-1 pollock declined, most likely from cannibalism by older pollock. There was also a shift in the distribution of age-1 pollock, with decreases in the southern part of the shelf, and increases in the northern shelf.

Responses of Marine Birds and Mammals

Information on the population dynamics of marine birds at colonies around the Bering Sea was recently summarized by Hunt and Byrd (1999). Since the mid-1970s, there has been a marked decline in the numbers of kittiwakes and murres breeding at the Pribilof Islands, whereas, at other colonies such as those at Cape Peirce in western Alaska, and Buldir Island in the western Aleutians, the numbers of kittiwakes and murres have been stable or increasing. Production of seabird young at the Pribilofs also declined precipitously between the 1970s and the early 1980s (e.g., Fig. 15) (Hatch, et al., 1993; Decker et al., 1995; Hunt et al., 1996b). However, it is not likely that the decrease in numbers of young produced caused the initial population declines. Because kittiwakes and murres do not recruit to the breeding population for two to four years after fledging, numbers of young produced through 1979 were probably adequate to sustain recruitment through 1982 at levels sufficient to prevent noticeable population declines. However, the decline in production would have affected the ability of the populations to rebound in later years (Hunt and Byrd, 1999; Byrd, unpublished).

Between 1975-79 and 1987-88, there were major shifts in the diets of murres and kittiwakes nesting at the Pribilof Islands (Decker et al., 1995; Hunt et al., 1996b,c). Capelin and the large pelagic amphipod, *Themisto libellula*, a cold-

water species, essentially dropped out of the diets of kittiwakes and murres on both islands, and the use of myctophids decreased for black-legged kittiwakes on St. George Island (Decker et al., 1995). The consumption of gadids, mostly age-0 and age-1 pollock, which in the 1970s had been a major portion of kittiwake and murre diets on both islands, also changed dramatically. There was a decrease in pollock in the diets of thick-billed murre chicks and black-legged kittiwakes, particularly after 1984 (Decker et al., 1995). Starting in 1978, there was also a replacement of age-1 pollock with age-0 pollock in seabird diets (Hunt et al., 1996c). Since the mid-1980s at the Pribilof Islands, sandlance (*Ammodytes hexapterus*) have become a more important component of kittiwake and murre diets than they were in the 1970s (Decker et al., 1995; Hunt et al., 1996b).

In the inshore waters of the shelf, Baduini et al. (2001a) show that short-tailed shearwaters (*Puffinus tenuirostris*), a transequatorial migrant that is the single largest contributor to marine bird biomass in the southeastern Bering Sea, shifted from diets dominated by adult euphausiids in the 1970s and 1980s to diets with a predominance of sandlance and age-0 pollock in the late 1990s. This shift may be recent. As recently as 1989, Hunt et al. (1996) found that shearwaters in August near the Pribilofs were taking only euphausiids, most of which were adult *T. raschii*. In June, 1997, adult *T. rashii* still predominated in shearwater diets, but in 1998 and 1999, the proportion of birds found with adult euphausiids declined. July and August samples of shearwaters from 1998 and 1999 lacked adult euphausiids, and instead showed broader diets dominated by fish (Hunt et al., this volume). High numbers of shearwaters starved in August-September 1997 (Baduini et al., 2001a), and in 1998, shearwaters were again emaciated, though no evidence of major mortality was found (Hunt et al., 1999; Baduini, 2000, Baduini et al., 2001b).

Among marine mammals, pinnipeds showed population declines and diet shifts similar to those found in breeding seabirds, whereas populations of baleen

whales appear to have increased. Opportunistic observations of Steller sea lions marked a steady decrease in numbers at Walrus Is., Pribilof Islands, between 1960 and 1980 (NMFS unpubl. data). Declines were particularly steep between 1975 and the early 1980s in both the number of animals on the island, and in the number of pups produced (Fig. 16). The Pribilof Islands population of northern fur seals, the pinniped with the highest biomass in the Bering Sea, was reduced to less than 10% of its historical population by over-exploitation in the early 1900s (Kenyon et al., 1954; Lander and Kajimura, 1982). Since the early-1950s, when the population had rebounded to about two thirds of its historical high of 3,000,000 animals, it has decreased by nearly one half (NMFS, 1993). Fur seal pup counts on the Pribilof Islands declined steeply between 1976 and the early 1980s (Fig. 17) (York et al., 2000). The decline continued until about 1981 on St. Paul Is., whereas on St. George Is. it continued until the mid- to late-1980s. The reduction in pup numbers on St. Paul Is. was about 33%, whereas on St. George Is., the reduction was about 60%. On the north side of the Alaska Peninsula, harbor seal (*Phoca vitulina*) numbers at haulouts have also decreased by about 50% (Fig. 18) (Withrow and Loughlin, 1995). However, there is no indication there was an abrupt drop in numbers in the late 1970s, as seen in the Steller sea lions and fur seals at the Pribilof Islands.

Large whales were almost extirpated in shelf waters of the eastern Bering Sea by the 1960s (NRC, 1996; Merrick, 1997). As of the mid-1970s, it was rare to encounter any large cetacean over the eastern Bering Sea shelf (Frost et al., 1982; Leatherwood et al., 1983; Brueggerman et al., 1987; Baretta and Hunt, 1994). Populations of large cetaceans appear to be rebounding in the eastern Bering Sea (Table 1; Baretta and Hunt, 1994; Tynan, 1998, 1999), and we may soon have the opportunity of assessing directly the role that they play in this ecosystem.

Diets of fur seals in the eastern Bering Sea changed dramatically between 1960 - 1974 and the 1980s and 1990s (Fig. 19). In the earlier period, diets were

spread evenly over a number of taxa, pollock averaged third among primary prey, and, although prey size was not measured at the time, most pollock were age-2 plus (Kajimura, 1984; Fiscus, pers. comm.). Capelin was an important, but inter-annually variable, part of fur seal diets between 1960 and 1974 (Kajimura, 1984). By the early 1980s, age-0 and age-1 pollock dominated the diets, Greenland turbot (*Reinhardtius hippoglossoides*) and capelin were no longer eaten, and sandlance increased in importance (Fig. 19) (Sinclair, 1988; Sinclair et al., 1994). Diets of fur seals on St. George and St Paul Islands were similar, except that St. Paul animals took more pollock and sandlance, and St. George animals took more squid, particularly species that tend to inhabit slope waters (Antonelis et al., 1997).

DISCUSSION

The time series reported here, as well as by others, document a number of significant changes in the marine ecosystem of the eastern Bering Sea since the mid-1970s (NMFS, 1993, 1995; NRC, 1996; Hare and Mantua, 2000; Schumacher et al., In Press). These changes include a massive increase in the biomass of walleye pollock, and lesser, but substantial, increases in Pacific cod, arrowtooth flounder, and rock sole (Livingston et al., 1999). There have also been major declines in the populations of fur seals, and Steller sea lions, and in the populations and reproductive output of some seabirds (kittiwakes and murre) at the Pribilof Islands (NMFS, 1993, 1995; Byrd and Dragoo, 1997; Hunt and Byrd, 1999). Declines in the fur seals and marine birds at the Pribilof Islands were accompanied by changes in diets. These changes indicated that forage fishes, in particular capelin, a species rich in fat, were less abundant after the late 1970s than was the case in the early- to mid-1970s (Sinclair, 1988; Sinclair et al., 1994, 1996; Decker et al., 1995; Hunt et al., 1996b,c; Merrick et al., 1996; Antonelis et al., 1997; Merrick, 1997).

The National Research Council (NRC) addressed some of the possible causes of these changes (NRC, 1996), as did Merrick (1995,1997). The time series reviewed in the present paper extend the record used by the NRC, and add new data sets. These data have enabled us to examine relative trends by locale. Importantly, we are able to show the marked spatial and temporal variation in the dynamics of populations in the southeastern Bering Sea, which provide new insights into the hypothesized mechanisms responsible for the decadal-scale changes noted above. Below we suggest a new hypothesis, the Oscillating Control Hypothesis, that provides a rationale for relating changes between top-down and bottom-up control in the eastern Bering Sea ecosystem to switches between warm and cold regimes.

Climate Change and Bottom-up Effects

The linkages between weather patterns and the timing and amount of primary production are strong. The timing of spring primary production is determined by a combination of the date of ice retreat, and the cessation of strong storm activity that permits stabilization of the water column (Fig. 6) (Sambrotto et al., 1986; Stabeno et al., 1998, 2001). If ice retreat comes before mid-March, then there is insufficient light to support an ice edge or under-ice bloom, and an open water bloom in May or June will result. The density structure of the water column in spring is primarily the result of thermal stratification, which begins in April and reaches a maximum in August. When spring winds are sufficiently strong to mix below the weak thermocline of April/May, the result is prolonged, moderate spring production, as occurred in 1998 (Stabeno et al., 2001). Post-bloom storms in spring and summer will result in mixing of nutrients from below the pycnocline, and a prolonging of the new production (Sambrotto et al., 1986; Whitledge et al., 1986). In 1975 and 1976, ice-associated blooms occurred (Alexander and Niebauer, 1981; Niebauer et al., 1990,1995) due to late ice retreat, whereas in 1979-1981, due to early ice retreat, open water blooms in May and June were encountered (Sambrotto et al., 1986). In the 1990s, a

mixture of ice-associated blooms (1995, 1997, 1999) and late, May and June, blooms (1996, 1998) have occurred.

The annual amount of new primary production is determined primarily by the amount of nutrients available in the upper mixed layer. If the pycnocline sets up quickly in the spring and is shallow and strong, the amount of nutrients available from cooler bottom waters for new production will be less than if the pycnocline is deep, or if it sets up gradually over a prolonged period. When the pycnocline is deep, more nutrients will be held in the photic zone. If the set up of the pycnocline is prolonged, multiple episodes of mixing will inject nutrients into the forming upper mixed layer.

There is no direct evidence that nitrate concentrations in the middle domain are less now than they were in the late 1970s and early-1980s. Profiles of nitrate concentrations in Whitley et al. (1986) are similar to those found in the late 1990s (Stockwell et al., 2001; Inner Front Project, Cruise Reports for spring 1998 and 1999). However, a single strong storm in spring can increase the availability of nutrients for production. For example, a severe storm in May, 1997, that mixed the water column to 55 m or more may have increased annual new production by up to 30% above levels measured in the early 1980s (Stockwell et al., 2001). Earlier ice retreat, and therefore later blooms dependent on weak thermal stratification, may lead to more frequent occurrences of prolonged production and likely larger amounts of total new production in spring. In contrast, calmer, sunnier summers with a warmer upper mixed layer will decrease the likelihood of injection of nutrients into the upper mixed layer by storms (Sambrotto et al., 1986), resulting in reduced summertime contribution to annual new production. Stockwell et al. (2001) report August/September values for production in 1997 considerably below those reported by Zeeman (1992) for 1988. However, when the upper mixed layer is depleted of particulate matter, there may be considerable sub-surface production, as occurred in the inner domain in 1997 and 1998 (T. Rho, Univ. Alaska, Fairbanks, Pers. Comm.).

Using the ratios of stable isotopes of carbon sequestered in the baleen of bowhead whales (*Balaena mysticetus*), Schell (2000) argued that there has been a trend toward decreased rates of primary production since the mid-1970s. Bowhead whales consume zooplankton in the Bering Sea during the fall and winter, and forage in the Beaufort Sea in spring and summer. Zooplankton obtained in the Bering Sea are likely to contain carbon derived primarily from phytoplankton consumed during the summer and fall, when they were growing. Thus, Schell may have evidence for decreased rates of summer and fall production rather than a decrease in total annual production. In addition, increases in water temperature or changes in the species composition of the phytoplankton may have influenced the change in $\delta^{13}\text{C}$ that he observed (Libes, 1992).

Lack of tight coupling between zooplankton production and primary production makes it particularly difficult to detect zooplankton (and fish recruitment) responses to variations in primary production (Runge, 1988). Instead, the biggest impact of interannual variability in production could be on the benthic communities of the shelf which are dependent on loose coupling between spring and summer new production and zooplankton grazing. Cold springs and summers punctuated with storms favor new production and a flux of large diatom cells to the benthos.

Walsh and McRoy (1986) interpreted the presence of a sub-surface chlorophyll maximum in the middle domain as evidence of transfer of phytoplankton to the benthos, and a lack of tight coupling between primary production and copepod grazing. Dagg et al. (1982) estimated that net-zooplankton grazing in 1979 accounted for 18% of daily phytoplankton production in the outer shelf and 25% in the middle shelf, whereas Cooney and Coyle (1982), also working in 1979, estimated that copepods consumed 20 to 30% of primary production in the outer domain and rarely >5% of primary

production in the middle domain. During a 15 year study of the eastern Bering Sea, including the shelf, between 1956 and 1970, Ikeda and Motoda (1978, in Cooney and Coyle, 1982) obtained grazing rates approximately 30% higher than those of Cooney and Coyle. These data suggest that there is considerable temporal variability in the strength of coupling between zooplankton and phytoplankton.

Water temperature exerts a strong influence on the growth rates of zooplankton (McLaren, 1963; Huntley and Lopez, 1992), and plays an important role in determining the fate of production (Vidal, 1980; Smith and Vidal, 1984, 1986; Vidal and Smith, 1986; Walsh and McRoy, 1986). Temperature is often thought of as more important than food availability for limiting the growth rates of small-bodied copepods (Corkett and McLaren, 1978; Vidal, 1980; Dagg et al., 1984). Thus, water temperature is likely to play a major role in interannual variation in copepod biomass in the middle domain where interannual environmental variability is greatest (Smith and Vidal, 1986; Baier and Napp, 2001).

Smith and Vidal (1986) compared spring zooplankton abundances in two relatively warm years (Fig 7), one of which was somewhat cooler (1980) than the other (1981). Over the middle shelf, spring abundances of *Pseudocalanus* and *Calanus* were higher in the warmer year. *Calanus marshallae*, a neritic copepod, produced two generations in 1981, but only one in the cooler year (1980). Coyle et al. (1996), in assessing Russian studies of zooplankton on the shelf, note that concentrations of *C. marshallae* and *Pseudocalanus* spp. on the middle shelf were denser in warmer years. Thus we may expect stronger coupling between zooplankton and phytoplankton in warmer years, all else being equal.

The timing of the spring phytoplankton bloom may also affect the fate of production, the composition of the zooplankton community, and the production of prey for larval fishes on the southeastern Bering Sea shelf. An ice-associated

bloom in March or early April may come too early, and at too low a water temperature, for zooplankton to make their maximum potential grazing impact. As zooplankton egg production is sometimes tied to food availability, early blooms in cold years may therefore lead to a mismatch between larval fish populations and the abundance of their preferred food (Napp et al., 2000).

The timing of the bloom may also influence the species composition of the copepod community. For example, during three recent years of contrasting climate conditions (1995 — 1997), *C. marshallae* began egg production well before the spring bloom, but copepodites did not appear until the onset of the bloom (Baier and Napp, 2001). This suggests that only those individuals that coincide with the spring bloom during the naupliar-copepodite transition survive. In 1980, a year with an open-water bloom in May, the copepod, *Pseudocalanus* spp., a numerically abundant component of the middle shelf zooplankton community, was relatively scarce until mid- to late-May (Smith and Vidal, 1986). If the principal or sole spring bloom had occurred in early April, as was the case in 1995, much of it might have fallen to the bottom before it could be grazed by *Pseudocalanus*, or gone to other species (Stabeno et al., 1998). With the trend toward the early retreat of ice in the spring, and a later spring bloom, a preponderance of spring production should occur in May and June, with more of the production available for copepods that are abundant in late spring.

In summary, the timing of ice retreat and the cessation of winter storms determine the timing of spring production. Timing and water temperature (which in spring are affected by sea ice) determine the fate of production, with relatively more of the production going to copepods in years when water is warm and the bloom is delayed and prolonged. This scenario is similar to that in the Barents Sea, where zooplankton are able to crop more of the primary production in years when water temperatures are relatively high (Loeng, 1989). When water temperatures are low and the spring bloom is early and brief, much of the primary production will fall to the benthos. Thus coupling between zooplankton

and phytoplankton is likely to be variable. If coupling between zooplankton grazing and primary production is weak, benthic food webs should be affected more by interannual variation in the timing, magnitude and duration of the spring bloom than the pelagic system. Prolonged summertime primary production may be critical for sustaining summer zooplankton populations and for transfer to fishes late in the season.

Climate Change and Upper Trophic Levels

The effect of climate on production and its fate are not a strictly a bottom-up process. Changes in water temperature influence the distribution of planktivorous fishes and their predators, affecting eventual top-down control of the distribution and abundance of prey and localized release of secondary and primary production.

Ice cover and water temperatures influence transfer of secondary production to predators. In the western Bering Sea, the year-class strength of cod is inversely associated with ice cover during the spawning period in early April (Vinnikov, 1996). Likewise, pollock in the eastern Bering Sea have stronger year-classes in warm years (Wespestad, 1991 in Balykin, 1996; Bulatov, 1995), particularly when spawning stocks are small (Khen, 1987, in Balykin, 1996) and when prevailing winds advect eggs and larvae away from adults (Wespestad et al., 2000). Pollock development and growth is accelerated in warmer waters (Haynes and Ignell, 1983; Nakatani and Maeda, 1984), possibly because of a higher abundance of their zooplankton prey, and because ice and cold temperatures cause a mismatch between the peak abundance of larval pollock and their prey (Napp et al., 2000). Quinn and Niebauer (1995) examined a variety of environmental variables and the recruitment of pollock at age-2. They found that the strongest relationships were with temperature during and after the first winter. Ohtani and Azumaya (1995) showed that mortality of pollock in their first winter is an inverse function of water temperature on the shelf. However, M ter et al. (1995) failed to find a statistically significant relationship between

water temperatures in the eastern Bering Sea and pollock year-class strength. This lack of correlation between year-class strength and temperature may be because predation on juveniles has become a more important regulator of year-class strength. Since the mid-1980s in the Gulf of Alaska, pollock recruitment has been more strongly controlled by flatfish and cod predation on juveniles than it is by environmental effects on larvae (Bailey, 2000).

Water temperature has a direct effect on the distribution of fishes. The horizontal and vertical distribution of pollock is sensitive to temperature (Bailey et al., 1999). Age-1 pollock avoid water colder than 2... C (Wyllie-Echeverria, 1996). During years of warm water temperatures and reduced ice cover, the cold pool shrinks and age-1 pollock extend their range northward (Wyllie-Echeverria, 1995). In winters with heavy ice cover in the eastern Bering Sea, age-1 pollock are more constrained to the southwestern portion of the shelf near the shelf edge, where they may be exposed to cannibalism by adult pollock (Dwyer et al., 1987; Ohtani and Azumaya, 1995; Wyllie-Echeverria, 1996).

Warming sea temperatures during the past decades could have played a significant role in the changes in fish distributions recorded here. Increasing water temperatures and decreasing ice cover may have facilitated the northward spread of pollock, Pacific cod, rock sole and arrowtooth flounder. Warmer temperatures also could have pushed capelin north from the vicinity of the Pribilof Islands, where they were formerly abundant. Capelin prefer cold water, and likely moved before pollock reached their highest densities. In the Barents Sea, capelin move large distances to stay in water masses with temperatures between -1 and $+2^{\circ}\text{C}$ (Loeng, 1989). According to Naumenko (1996), capelin in the Bering Sea will avoid water above 2°C and will migrate considerable distances to avoid warmer near-bottom waters. In 1976, bottom temperature near the Pribilofs was about 0°C , whereas in 1977, the temperature was 3°C (Overland et al., 1999). Although water temperatures near the bottom declined to below 2°C in the early 1980s, by then a large biomass of adult pollock was

present and they may have prevented the local recovery of capelin stocks. Trawl surveys by the National Marine Fisheries Service obtained a plentiful bycatch of capelin near the Pribilof Islands in summer 1975, but not in 1978 or years thereafter (Hunt et al., 1996b; Brodeur et al., 1999b).

From the Top down

Consumption of zooplankton by fish is a limiting factor in the impact of zooplankton grazing on phytoplankton. The estimates of zooplankton grazing rates by Dagg (1982) and Cooney and Coyle (1982) may be low compared to those in years with small year-classes of pollock. These observations were conducted in a year (1979) of unusually high abundance of age-1 pollock, and predation by juvenile pollock in that year may have limited copepod grazing more severely than usual. Springer (1992) estimated that pollock should consume virtually all of the secondary production in the middle and outer domains. In recent years (1994-1999), an inverse relationship between zooplankton biomass and age-0 pollock abundance has been observed at the end of summer around the Pribilof Islands (Swartzman et al., this volume). Sugimoto and Tadokoro (1998) have shown that there is a biennial fluctuation of zooplankton biomass in the Bering Sea that is negatively correlated with the catch of Asian pink salmon (*Oncorhynchus gorbuscha*). Likewise Tadokoro et al. (1996) found a negative relationship between the volume of stomach contents in chum salmon (*O. keta*) and the numbers of pink salmon in the central Subarctic Pacific Ocean and the Bering Sea. These results suggest a closer coupling between grazing by planktivorous fishes and zooplankton biomass than between zooplankton grazing and primary production. In particular, in years of high planktivore abundance, zooplankton production is hypothesized to limit fish production and survival.

Stockwell et al. (2001) found greater densities of *Acartia* spp., *Pseudocalanus* spp. and *C. marshallae* in June, 1997, a year with a cold early spring, compared to densities in June 1981 a warm year, the opposite of what one might have expected if temperature alone was controlling zooplankton

production. The elevated populations in 1997 may have been facilitated by a reduction in predation pressure. The abundance of age-0 pollock over the southeastern shelf was relatively low in 1997 (Swartzman et al., this volume).

Sockeye salmon (*O. nerka*) have the potential to impact the biomass of euphausiids over the shelf. The tributaries of Bristol Bay support the largest fishery for wild sockeye salmon in the world. The Bristol Bay catch of these fish varied from 5 to 20 million fish for most of the period between 1900 and 1970 (Kruse, 1998). As of 1975, catches surged from less than 5 million fish to 25 million fish in 1980 and 1981, and 35 million in 1983. In 1997 and 1998, the catch declined to 12.1 million fish and 9.7 million fish, respectively, as compared to the previous ten year average of 30.0 million fish.

Sockeye salmon go to sea after 1 to 3 years in fresh water (Kruse, 1998). In the southeastern Bering Sea, they migrate along the north side of the Alaska Peninsula in spring as they make their way to the North Pacific Ocean via passes through the Aleutian Islands. Adults return to breed in the rivers of Bristol Bay, with most of the fish arriving between the last week of June and the first week of July (Nishiyama, 1972). Over the shelf in Bristol Bay, euphausiids constituted 70% of their diet and larval fish (mostly sand lance) constituted 20% of the diet by weight. If we assume an average daily demand of 81 kcal per 2.2 year old sockeye in Bristol Bay (the average value from Nishiyama (1972) Table 15.13), then the daily consumption would be approximately 43 g wet weight of euphausiids per fish. In 1981, 25 million salmon would have consumed 1.1×10^3 metric tons of euphausiids daily, whereas in 1996, 45 million fish would have consumed about 2×10^3 metric tons daily. This consumption may have been partially responsible for the rapid seasonal decrease in euphausiid abundance recorded by Smith (1991) in April and May of 1980 and 1981.

The fauna of the Bering Sea ecosystem is very different now than it was prior to the beginning of large-scale commercial whaling and fishing. By

removing vast quantities of whales, pinnipeds, fish and shellfish, human activities have exerted a top down effect on the marine ecosystem and changed the relative abundance of species, possibly opening the way for a single species, the walleye pollock, to dominate the pelagic biomass (Sinclair, 1988, Sinclair et al., 1994, 1996; NRC, 1996; Merrick, 1995, 1997).

Walleye pollock show a strong negative relationship between adult biomass and year-class strength (eastern Bering Sea: $r = -0.70$, Wespestad, 1994; western Bering Sea: $r = -0.81$, Balykin, 1996) that is related to cannibalism (Wespestad and Quinn, 1996). In the southeastern Bering Sea, most of the biomass of age-1 pollock is gone from the shelf, particularly in the southern portion and around the Pribilof Islands. When changes in the biomass of age-1 and age-2-plus pollock have been out of phase, declines in age-1 pollock appear to have occurred when the CPUE of age-2-plus pollock exceeded 50 kg/ha in the trawl surveys (e.g., Fig 14, Pribilof Islands, South Outer Shelf, North Middle Shelf). However, the trawls provide only an index of the biomass of the age-1 fish and the wide variability in year-class strength frustrates rigorous testing of whether there is a threshold density for age-2-plus pollock, above which age-1 pollock decline. Only over the North Outer Shelf do age-1 pollock remain generally abundant, though abundance levels vary widely. This stratum has some of the highest densities of age-2-plus pollock, and may be a sink for age-1 pollock if they migrate there from elsewhere on the shelf. Increases in cod and flatfishes, in particular arrowtooth flounder, may also be having a negative effect on the survival of juvenile pollock in the Bering Sea, as do northern fur seals (Lang et al., 2000; Livingston and Jurado-Molina, 2000). In the Gulf of Alaska, predation has also become the most important determinant of juvenile pollock survival (Bailey, 2000).

According to the Trophic Cascade Hypothesis, the removal of a large biomass of predators should release an amount of prey equivalent to the consumption demands of the missing predators (Merrick, 1995, 1997). Age-1

pollock consume copepods and euphausiids, as well as age-0 pollock (Grover, 1991; Livingston and Lang, 1996; Lang et al., 2000). The declines of age-1 pollock and capelin over the shelf of the southeastern Bering Sea should have greatly decreased the consumption of zooplankton there. Likewise, declines in the abundance of adult pollock over the southern shelf should have released large amounts of zooplankton from predation (Livingston and Lang, 1996). In addition, the marked drop in sockeye salmon returns in 1997 and 1998 should have released euphausiids along the Alaska Peninsula from considerable predation pressure in those years. However, except for the data of Stockwell et al. (2001), there is little evidence of an increase in crustacean zooplankton over the shelf.

Two sources of predation on zooplankton increased between the 1980s and 1997-1999: Large scyphomedusae, which eat zooplankton as well as small fish, have increased exponentially since the late-1980s (Brodeur et al., 1999, ms). One jellyfish species, *Chrysaora melanaster*, alone was estimated to consume about a third of the zooplankton standing stock around the Pribilof Islands in 1999, compared to a consumption of < 1% in 1982 (Brodeur et al., ms). This increase may be the result of release from competition with age-1 pollock, or it may reflect warming sea temperatures. In most strata, increases in bycatch of jellyfish increased after a decline in age-1 pollock (Fig. 9). Baleen whales have also increased over the shelf (Baretta and Hunt, 1996; Tynan, 1998, 1999; Hunt unpubl. data). Humpback whales were apparently more abundant in the Bristol Bay area in 1997-99 than in recent decades (Tynan, 1998). Groups of 9 to 12 were encountered each year from 1997 to 1999 in the inshore waters of Bristol Bay from the Port Moller area around to Togiak Bay (Hunt, unpublished). Diet composition of the whales is not known, but when encountered, they were usually feeding in the immediate vicinity of shearwaters that were taking euphausiids. Shearwaters, which in the Bristol Bay region formerly took euphausiids almost exclusively, died of starvation in huge numbers in 1997 and shifted their diets to include fish (Baduini et al., 2001).

Since the late 1970s, kittiwake and murre populations have declined at the Pribilof Islands and have shown reduced production of young (Hunt and Byrd, 1999). The most likely explanation for these changes is a decline in the abundance of forage fishes. Pribilof birds no longer obtain fat-rich capelin, and similarly-sized, though fat-poor, age-1 pollock have become scarce (Fig. 14, Decker et al., 1995; Hunt et al., 1996b,c). Use of age-0 pollock and sandlance has increased. Sandlance are smaller and less fatty than capelin, and seabirds have higher reproductive success when using capelin (Baird, 1990). Similarly, at the Pribilof Islands, populations of northern fur seals and Steller sea lions have declined (Fig. 16 and 17) (NMFS, Unpubl. Data; Loughlin et al., 1994). As with the marine birds there, fur seals also showed changes in their diets. Capelin were no longer taken as of the early 1980s, and there was a shift from large pollock to age-0 and 1-year-old pollock in the diets as of the 1980s (Fig 19) (Sinclair, 1988; Sinclair et al., 1994, 1996, Fig. 7).

In contrast to the situation in the Pribilof Islands, populations of these marine birds and northern fur seals have thrived in the western Aleutians and seabird populations have remained steady along the west coast of Alaska (Antonelis et al., 1991; Ream and Towell, 1998; Hunt and Byrd, 1999). Fur seals and seabirds in the Aleutian Islands, and seabirds along the Alaska coast, are dependent on food webs that differ from those used on the Pribilof Islands in that they are not dominated by pollock (Antonelis et al., 1997; Springer, 1996; Springer et al., 1996). The decline of harbor seals along the coast of Bristol Bay suggests that at some season, they use a food web different from the seabirds nesting on the shores of Bristol Bay which have not declined.

Synthesis.

Based on the available time series and process studies, several relationships appear to be important in governing production and its fate in the southeastern Bering Sea:

- 1) The timing and duration of ice cover and winter winds determines the onset of springtime net primary production.
- 2) The amount and timing of spring and summer storm activity, coupled with thermocline strength, determine the amount of annual new production.
- 3) Water temperature and grazing by forage fish control the biomass of zooplankton. All else being equal, warm water years, and/or years with prolonged springtime production, should support a larger biomass of zooplankton than cold water years or years in which production is confined to a brief, intense early pulse.
- 4) In years of high planktivore abundance, zooplankton stocks are reduced by predation.
- 5) In recent years when the biomass of adult pollock and other large predatory fish has been high, predation by large predatory fish has strongly influenced pollock year-class strength.
- 6) Other than the fisheries harvest, the availability of forage fish and other prey determine the biomass of adult pollock and that of other large predatory fish.
- 7) Food availability, rather than predation, controls the populations of marine birds, whales and most likely pinnipeds in the Bering Sea.

The following view of the Bering Sea builds on conceptual models proposed by Saetersdal and Loeng (1987), Loeng (1989), Beamish (1993), Bulatov (1995), and Bailey (2000) for other ocean regions. We suggest that an important feature of the southeastern Bering Sea marine ecosystem is the potential for weak coupling between components and for rapid non-linear shifts in response to physical forcing, as is most evident in the timing of primary production in the spring, and weak coupling between phytoplankton and zooplankton. We also suggest that there may be abrupt shifts between top-down and bottom-up control. Rather than arguing for either top-down or bottom-up control, we suggest that both forcing mechanisms are likely to operate, but in

strongly different proportions depending on climate regime (Roff et al., 1988; Reid et al., 2000)

The coupling between forage fishes and zooplankton, and between forage fishes and large predatory fishes may be either top-down or bottom-up. Two factors control these relationships: (1) If large picivorous fishes are sufficiently abundant, the control will be top-down, and forage fish production and biomass will be uncoupled from zooplankton production. In this case, zooplankton may be abundant and more strongly coupled to phytoplankton than when forage fish crop down zooplankton populations. (2) If populations of large predatory fish are scarce, larval fishes and forage fishes will be subject to less severe predation pressure. Therefore, the abundance of zooplankton will play an important part in pollock year-class strength and the control will be bottom-up. In this case, forage fish will depress zooplankton stocks, and zooplankton are likely to be uncoupled from phytoplankton production. Water temperature will affect zooplankton production as well as the survival of fish eggs and larvae. However, only when large predatory fish are scarce and unable to exert significant predation pressure will temperature have an effect on forage fish biomass via its effect on zooplankton growth.

Thus, we suggest a new hypothesis, the Oscillating Control Hypothesis, as an approach for understanding decadal-scale change in the southeastern Bering Sea. During cold regimes (with cold water in spring and summer), zooplankton should be in short supply, and year-class strength for pollock should be weak. Under this regime, recruitment to the adult pollock population will be weak because the system is constrained by bottom-up processes. During warm regimes (with warm water in spring and summer), there should be consistently strong production of zooplankton, and the potential for large year-classes of pollock based on good survival of larval and juvenile fishes. The increased frequency of large year classes since the switch to a warm regime in 1976/77 is consistent with this prediction (Hollowed et al., 1998). However, as the warm

regime continues over time, the biomass of adult predatory fishes will increase, and control will switch to top-down (e.g. Bailey, 2000). When forage fishes are strongly limited by top-down processes, there should be more zooplankton to support other planktivore populations. Thus, periods of high biomass levels of pollock and salmon might be expected to overlap, as has been the case until recently. Our hypothesis differs from that of Sugimoto and Tadokoro (1998) in that they propose that bottom-up controls work at the decadal-scale, whereas top-down controls work at a biennial or annual-scale.

The speed and effects of shifts from one regime type to another are likely to be asymmetrical. When there is a shift from a cold regime to a warm regime, zooplankton food will be plentiful for larval and juvenile fishes, and predation from adults should be weak for several years. Thus, there should be an almost immediate surge in forage fish and pollock year-class strength due to high larval and juvenile survival (e.g., 1978 and up to 3 years following). In contrast, after a shift from a warm to a cold regime, it will take some time for the populations of adult predatory fish to decline sufficiently that control can shift from top-down to bottom-up (possibly what has been occurring since 1998).

Interannual variation in forage fish and pollock year-class strength can be expected within warm regimes, in large part because of the spatial patterns of distribution of adult predators and forage fishes. As the populations of adults redistribute themselves seeking preferred water temperatures, there will occur areas temporarily free of predators. If adequate zooplankton resources are available in these pockets, larval and juvenile survival will be high. Wespestad et al. (2000) have suggested a mechanism for inshore transport of larval and juvenile pollock which can lead to segregation from cannibalistic adults and the potential for strong year-classes.

These hypotheses suggest a number of relationships that should hold if the hypotheses are correct:

- 1) If the timing of spring primary production is determined by the extent of ice cover and the timing of ice retreat and winter winds there should be an abrupt shift from early ice-associated blooms to late spring blooms as a function of the date of ice retreat. On-going monitoring studies with biophysical moorings are developing the time series necessary for testing this relationship.
- 2) If the amount of new primary production is tied to spring and summer storm activity, then there should be a correlation between the amount of storm mixing and the draw-down of nutrients at depth over the shelf. Monitoring of nutrients available at the end of winter and again in fall should provide data for testing this relationship, as should a more ambitious project to understand the mechanisms of cross-shelf transport.
- 3) If zooplankton production is decoupled from primary production, then we should see interannual and interdecadal variation in zooplankton biomass tied to either water temperature or predator demand, but not to annual primary production rates. However, variability in the flux of phytoplankton to the benthos should be strongly correlated with spring primary production. Since measurement of annual rates of primary production is difficult, comparison of variation in spring sedimentation rates with zooplankton biomass may be instructive. Testing these relationships will require development of a rigorous time series of zooplankton biomass over the shelf, and monitoring with sediment traps.
- 4) If forage fish grazing controls zooplankton biomass and the strength of coupling of zooplankton to phytoplankton, we should an inverse relationship between the strength of coupling between zooplankton and phytoplankton and the abundance of forage fish. To evaluate these relationships, we need a representative sample of the grazing pressure exerted by zooplankton on phytoplankton

under different levels of forage fish predation. The studies of zooplankton grazing by Dagg et al. (1982) were conducted in 1979, when the large 1978 year-class of pollock would have decreased zooplankton biomass and thus grazing pressure. We lack data from years when forage fish were scarce, and coupling between zooplankton and phytoplankton might have been expected to be stronger. More information is also required about the consumption of zooplankton by larval fishes (e.g., Dagg et al., 1984; Hilgruber et al., 1995; Napp et al., 2000), and juvenile pollock (Ciannelli et al., 1998) and other forage fishes under a variety of temperature and prey-density regimes.

- 5) In warm regimes, the biomass of adult pollock and other predatory fish should be high, and these predators will compete with other apex predators such as pinnipeds and marine birds for forage fish, with the result that bird and pinniped populations may decline. In cold regimes, once the biomass of adult pollock and other predatory fish have declined, competition for forage fishes may favor pinnipeds and marine birds, and their consumption of young pollock may slow recovery of pollock biomass.
- 6) If the numbers of large cetaceans continues to increase, their grazing of zooplankton should impact the availability of zooplankton for other planktivores. This grazing should create a new route for top-down control that affects the middle of the food web, rather than competing directly with large piscivorous fishes for forage fishes. If they consume large quantities of larval and juvenile forage fishes, cetaceans will compete directly with apex predators such as seabirds and pinnipeds. We need more information about the distribution, biomass, prey consumption and dietary composition of these large cetaceans if we are to evaluate their impact on the ecosystem. Observation of other top predators, such as seabirds

or pinnipeds, may provide useful insights into the impact of whales on the availability of zooplankton and juvenile fishes.

Where do the late 1990s fit in?

The eastern Bering Sea presented SEBSCC and Inner Front Project researchers with an ecosystem in 1996-1999 that was very different from that described in the mid-1970s and, to a lesser extent, also different from the ecosystem described in the late 1970s and early 1980s. Between 1996 and 1998, the eastern Bering Sea was generally more ice-free, and had longer and calmer summers with a warmer upper mixed layer than before. In contrast, 1999 was similar to the 1975/1976 period, with cold temperatures, late departure of ice, and stormy weather. Thus, a characteristic of the late 1990s was great interannual variability. The warmest summertime sea surface temperatures recorded since the 1960s occurred in 1997, and one of the coldest years on record was 1999. Integrated heat in the water column was highest in 1998, in part because heat stored in the water column from the previous year was not completely removed. Evidence for stronger-than-usual cross-shelf advection was present in the summers of 1998 and 1999.

In addition to physical differences, there were also marked differences in biological processes in the 1990s compared to what had been found in earlier studies. In the late 1990s, coccolithophore blooms dominated the phytoplankton in summer (Sukhanova and Flint, 1998; Vance et al., 1998; Napp and Hunt, 2001, Stockwell et al., 2001). The responses of the crustacean zooplankton are not clear. There appear to have been more copepods present in the late 1990s, but there is little evidence of dramatic change in euphausiid numbers. By the 1980s, upper trophic level organisms changed dramatically in abundance and, where studied, in diet. The biomass of large predatory fish surged, while at the same time the biomass of forage fish declined, particularly over the southern shelf. In the late-1990s, the biomass of large predatory fish appeared to decline. The biomass of jellyfish and baleen whales increased between the mid-1970s

and the late-1980s, though the increases in their numbers came later, possibly as late as the early-1990s for jellyfish. Populations of piscivorous marine birds and pinnipeds declined, particularly in the vicinity of the Pribilof Islands.

From a bottom-up perspective, the physical forcing factors resulted in new production coming early in the year (1995, 1997 and 1999). At the same time, cold water temperatures early in spring would not have favored transfer of production to pelagic zooplankton. From a top-down perspective, it appears that the increase in predatory fish biomass decreased forage fish consumption of zooplankton, with some of the biomass released being taken by jellyfish and whales. The availability of forage fish to pinnipeds and marine birds remained low. The impact on pinnipeds and marine birds was particularly acute at colonies around which populations of both forage fish and, more recently, age-2-plus pollock have declined. The whales may once again become important consumers on the shelf, but the impact of their foraging on zooplankton (and age-0 pollock?) has yet to be measured.

If spring and summer water temperatures are key to the productivity of zooplankton, and the degree and direction of coupling between zooplankton and forage fish are key to the support of adult pollock and other apex predators, we need to refocus our energies on these parts of the food web. Knowledge of zooplankton coupling to juvenile pollock and other forage fish is critical, as is understanding the role of apex predators other than pollock in this ecosystem. An ecosystem approach to management of the Bering Sea is of great importance if all of the ecosystem components valued by society are to thrive. Cognizance of how climate regimes may alter relationships within this ecosystem will facilitate reaching that goal.

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Table 1. Changes in the number of cetaceans sighted in 1975 — 1978 and 1987-1989 near the Pribilof Islands. Data from Baretta and Hunt (1994).

Survey Effort Taxon	Time Period			
	1975-1978		1987-1989	
	3867 km		6101 km	
	Individ.	Individ/500 km	Individ.	Individ/500 km
Fin Whale	0	-	66	5.4
Minke Whale	3	0.4	38	3.1
Humpback Whale	0	-	24	2.0
Orca	5	0.6	58	4.7
Unidentified Whale	0	-	70	5.7
TOTAL WHALES	8	1.0	256	21.0
Dall's Porpoise	101	13.1	241	19.7
Unidentified Porpoise	7	0.9	1	0.1
TOTAL PORPOISES	108	14.0	242	20.0

Figure Legends

Figure 1: The southeastern Bering sea shelf, with the strata into which the data from the National Marine Fisheries Service bottom trawl surveys were binned. The eastern edge of the North and South Middle Shelf approximate the 50 m isobath, the western edges of the North and South Middle Shelf approximate the 100 m isobath, except at the Pribilof Islands, and the western edge of the North and South Outer Shelf and Pribilof strata approximates the 200 m isobath.

Figure 2. The Pacific Decadal Oscillation (PDO8, after Mantua et al., 1997) and the Arctic Oscillation (after Overland et al., 2000).

Figure 3: Percent concentration of sea-ice over the eastern Bering Sea Shelf within two bands of latitude, 59 to 60 ... N and 57 to 58 ... N. Note the preponderance of earlier dates for ice-free water since 1975 in the more southerly region. Also note the longer duration of ice cover since fall 1998.

Figure 4. Contours of the number of weeks that sea-ice was present over the over the eastern Bering Sea shelf. The data were divided into three periods, representing the three regimes a) 1972-1976 b) 1977-1989 c) 1989-1998. (After Stabenow et al, 2000, Figure 5).

Figure 5: Wind speed cubed at St. Paul Island, 1955 to 1999.

Figure 6: Timing of the last retreat of significant ice cover, the timing of the shift from winter wind conditions to summer winds, and their effect on the timing of the spring bloom in the central portion of the middle domain. Note that ice-related or early blooms occur in years when the ice retreat comes in late March or later. Early ice retreats lead to May or June blooms. The date of the last winter storm was defined as when the wind speed cubed fell below $2500 \text{ m}^3 \text{ s}^3$ for the summer. The winds were measured at St. Paul Island.

Figure 7: Time-series of seasonal changes in sea surface temperatures in the South Middle Shelf stratum, based on the GISST data set produced by the United Kingdom Meteorological Office (UKMO) (Parker et al., 1993).

Figure 8: Changes in zooplankton biomass at stations in regions of the Outer, Middle and Inner domains of the southeastern Bering Sea repeatedly sampled during the Oshoro Maru Summer Cruises. Data from 1977 to 1994 from Sugimoto and Tadakoro (1997). Data from 1995 to 1999 from Dr. N. Shiga, unpublished.

Figure 9: Comparison of the trends in catch per unit effort for jelly fish and the three-year running mean for forage fish, by stratum in the southeastern Bering Sea. See figure 1 for location of strata.

Figure 10: Top: Changes in the catch per unit effort of Pacific cod and age-2 plus walleye pollock, combined, in the National Marine Fisheries Service (NMFS) bottom trawl surveys. Area covered includes all strata. Smoothed line is a three-year running mean.

Middle: Changes in the catch per unit effort of flatfishes, including rock sole, yellowfin sole and arrowtooth flounder in the NMFS bottom trawl surveys. Area covered includes all strata. Smoothed line is a three-year running mean.

Bottom: Changes in the catch per unit effort of forage fishes, including age-1 pollock, age-1 Pacific cod, Pacific herring, eulachon, and capelin in the NMFS bottom trawl surveys. Area covered includes all strata. Smoothed line is a three-year running mean.

Figure 11: Changes in the catch per unit effort of age-2 plus pollock in the NMFS bottom trawl surveys by stratum in the southeastern Bering Sea. See Figure 1 for location of strata.

Figure 12: Changes in the catch per unit effort of arrowtooth flounder in the NMFS bottom trawl surveys by stratum in the southeastern Bering Sea. See Figure 1 for location of strata.

Figure 13: Changes in the catch per unit effort of northern rock sole in the NMFS bottom trawl surveys by stratum in the southeastern Bering Sea. See Figure 1 for location of strata.

Figure 14: Comparison of the trends in catch per unit effort for age-1 pollock and age-2 plus pollock, by stratum in the southeastern Bering Sea. See Figure 1 for location of strata.

Figure 15: Comparison of the rates of chick production of black-legged kittiwakes at three colonies and of red-legged kittiwakes at two colonies. St. Paul and St. George Islands, are in the Pribilof Islands; Cape Peirce is on the coast of western Alaska at about the same latitude as the Pribilof Islands.

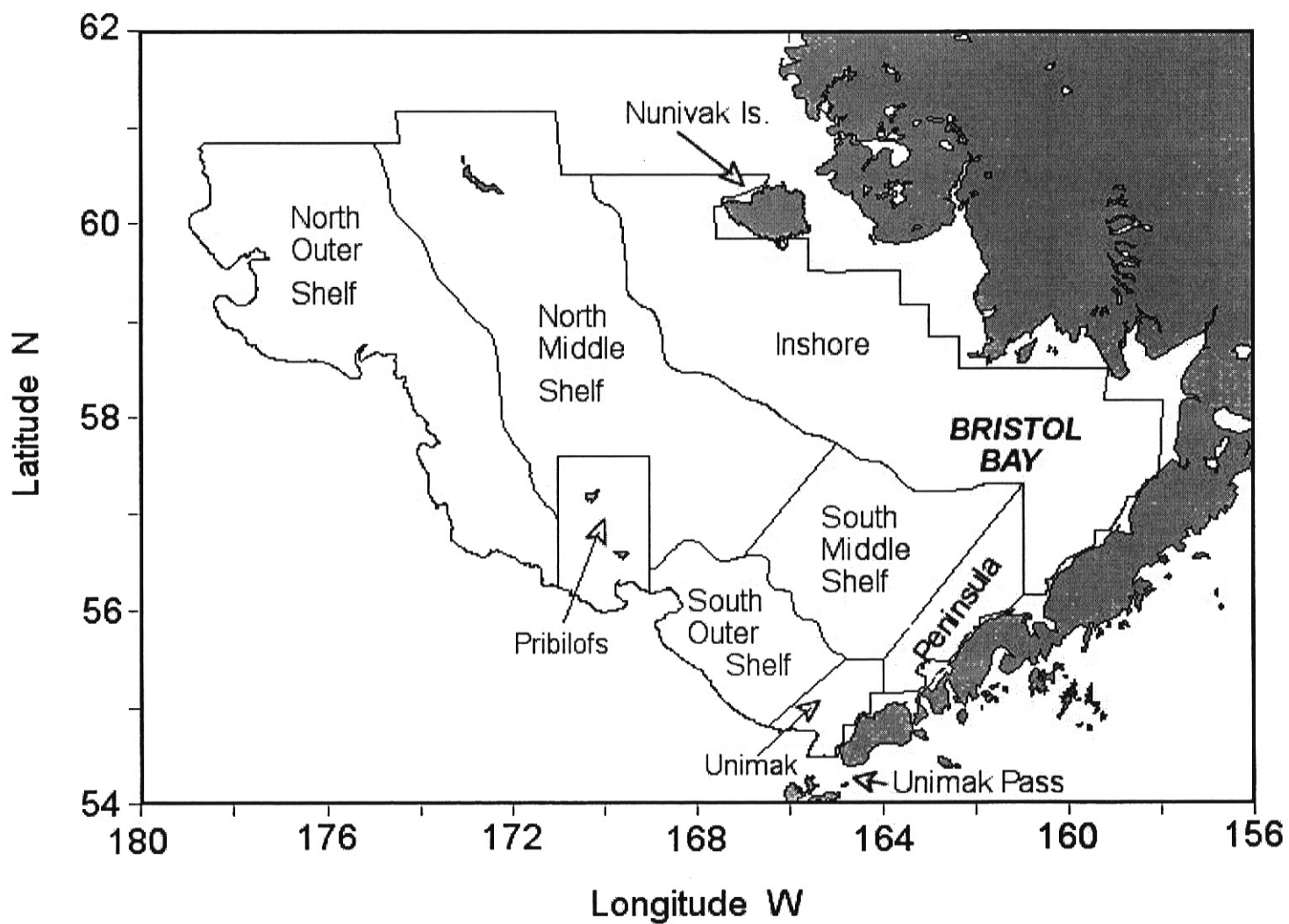
Figure 16: Comparison of counts of Steller sea lion pups and adult Steller sea lions on Walrus Island, Pribilof Islands.

Figure 17: Counts of northern fur seal pups at rookeries on St. Paul and St. George Islands, Pribilof Islands.

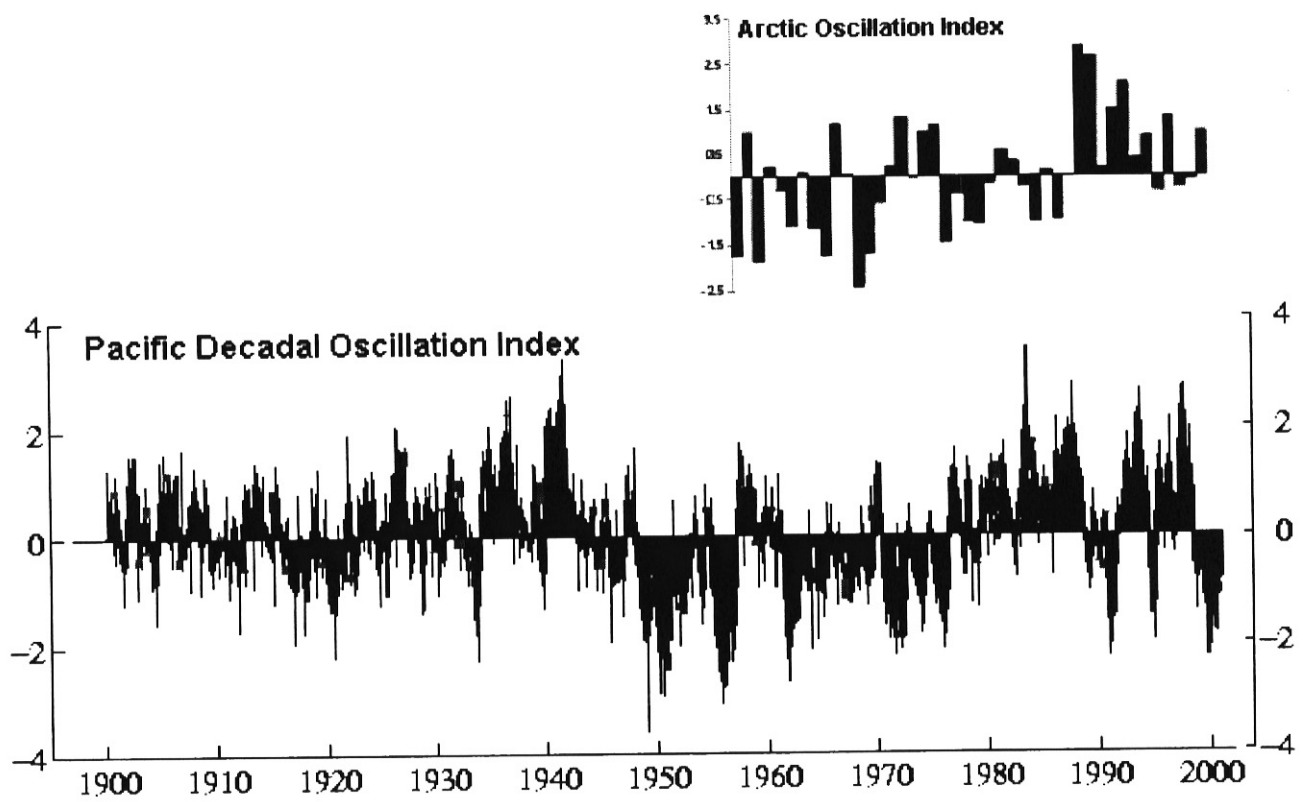
Figure 18: Harbor seal numbers at haulouts on the north side of the Alaska Peninsular. Line is the best fit, least squares regression.

Figure 19: Changes in the diets of northern fur seals collected in pelagic sampling near the Pribilof Islands, and from scats on the rookeries. Data for northern fur seal diet data for pelagic collections in 1960-1974 were derived from

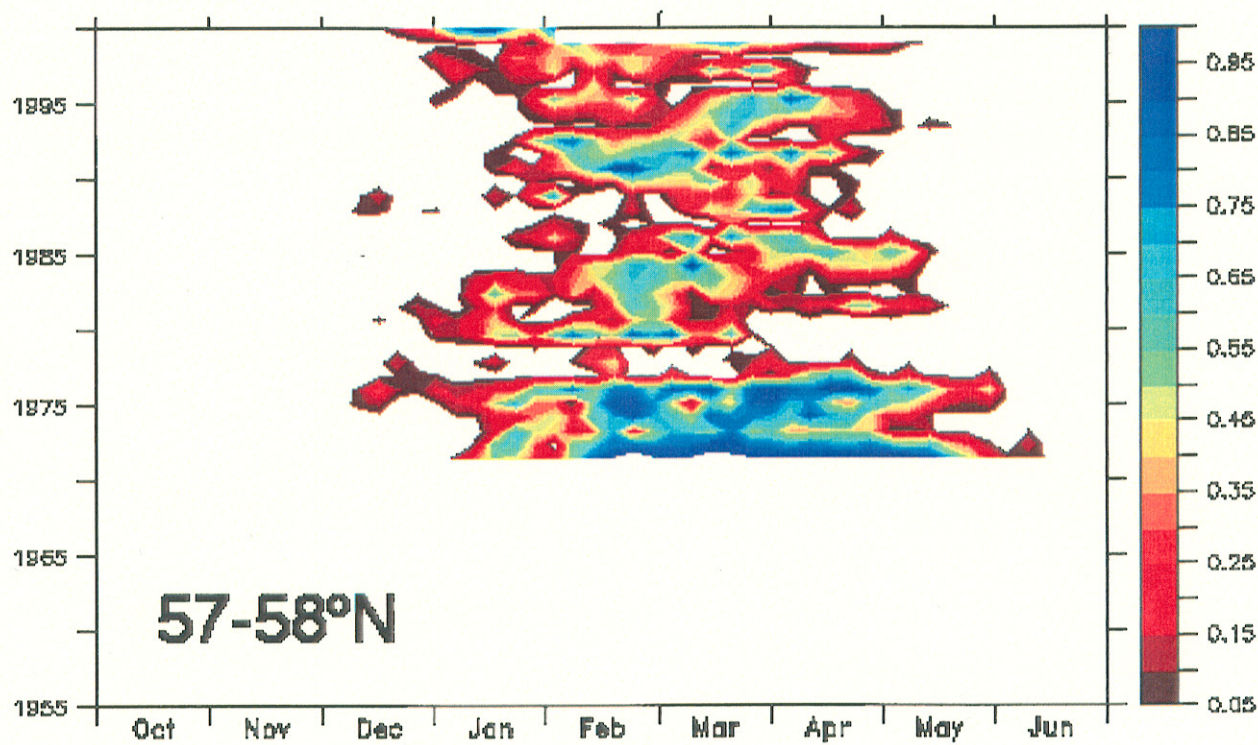
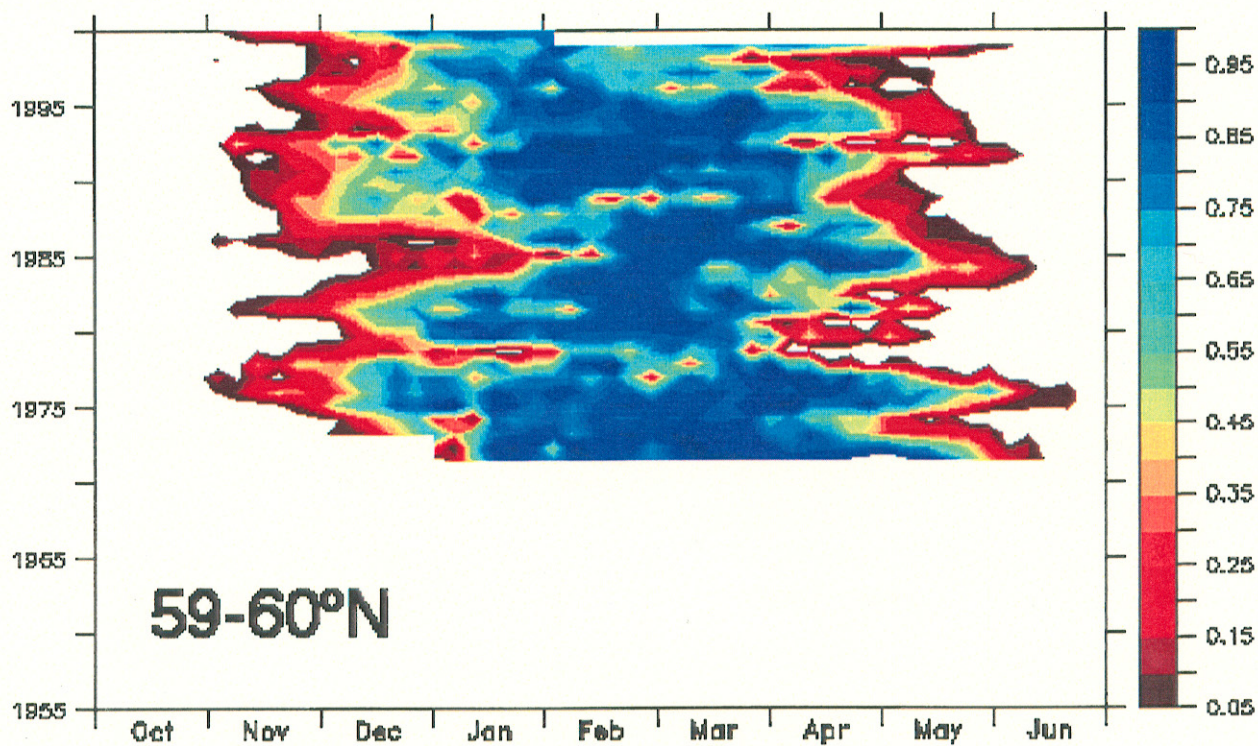
Kajimura (1984). Data for pelagic collections in 1981, 1982, and 1985) are from Sinclair 1988 and Sinclair et al. 1996. The St. Paul and St. George Island data are from Antonelis et al. (1997).



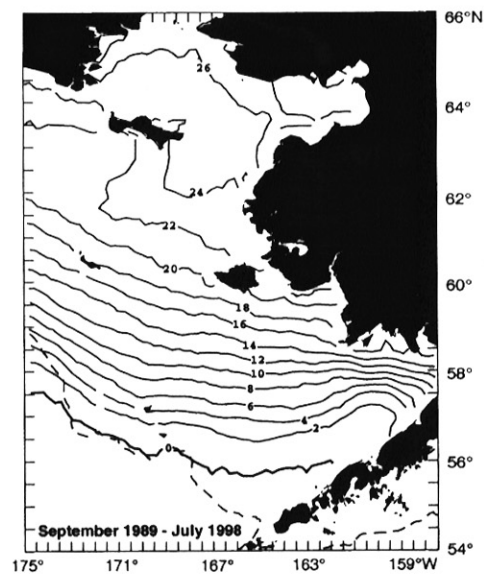
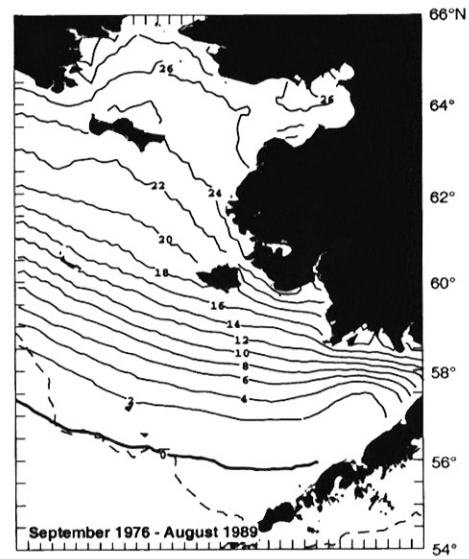
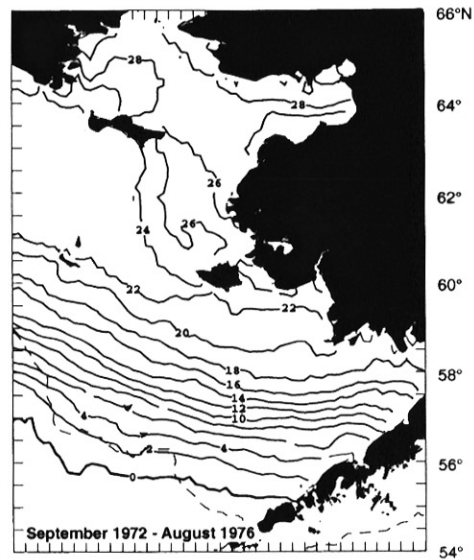
Hunt et al., Fig 1



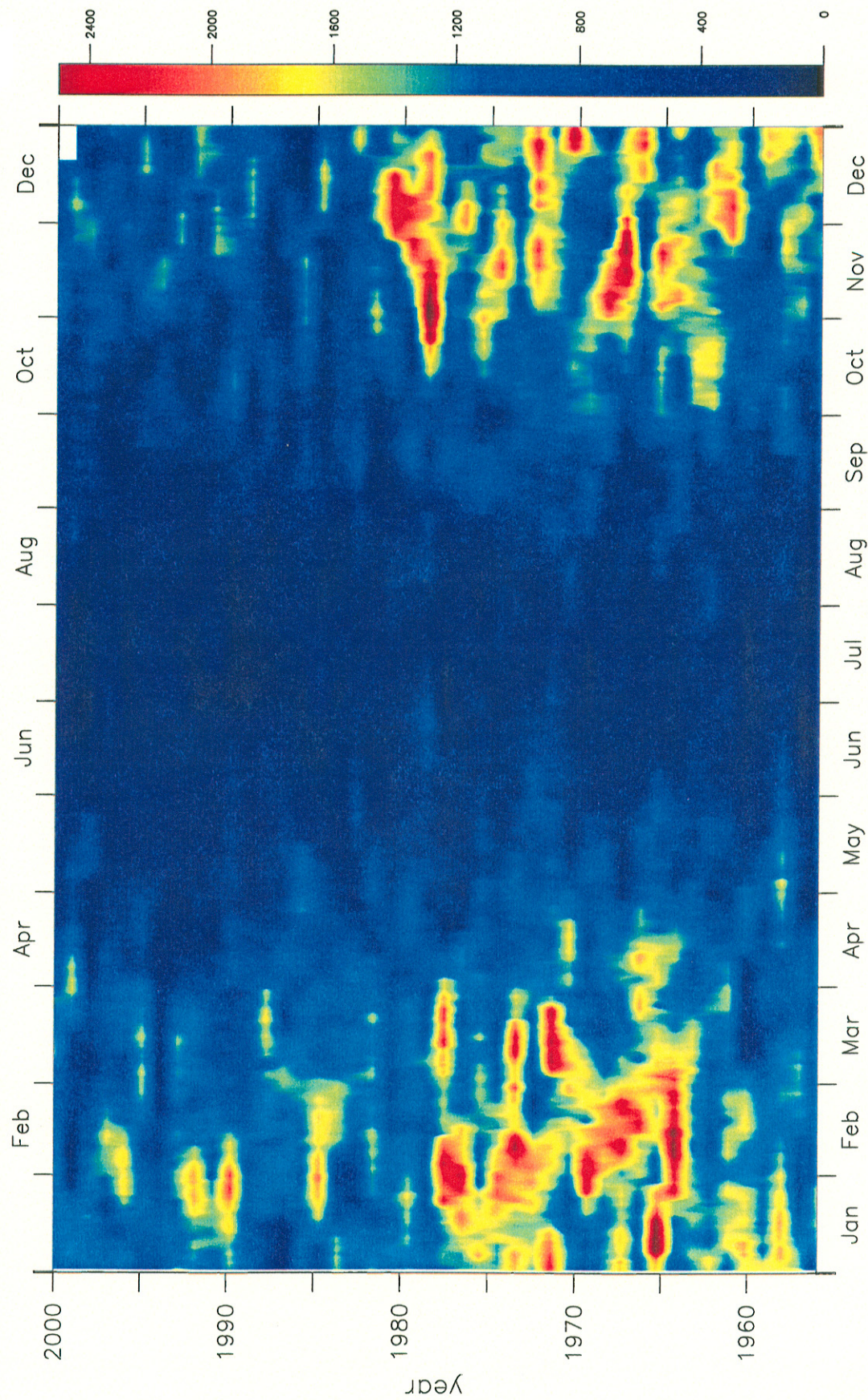
Hunt et al. Fig. 2



result of Fig 3



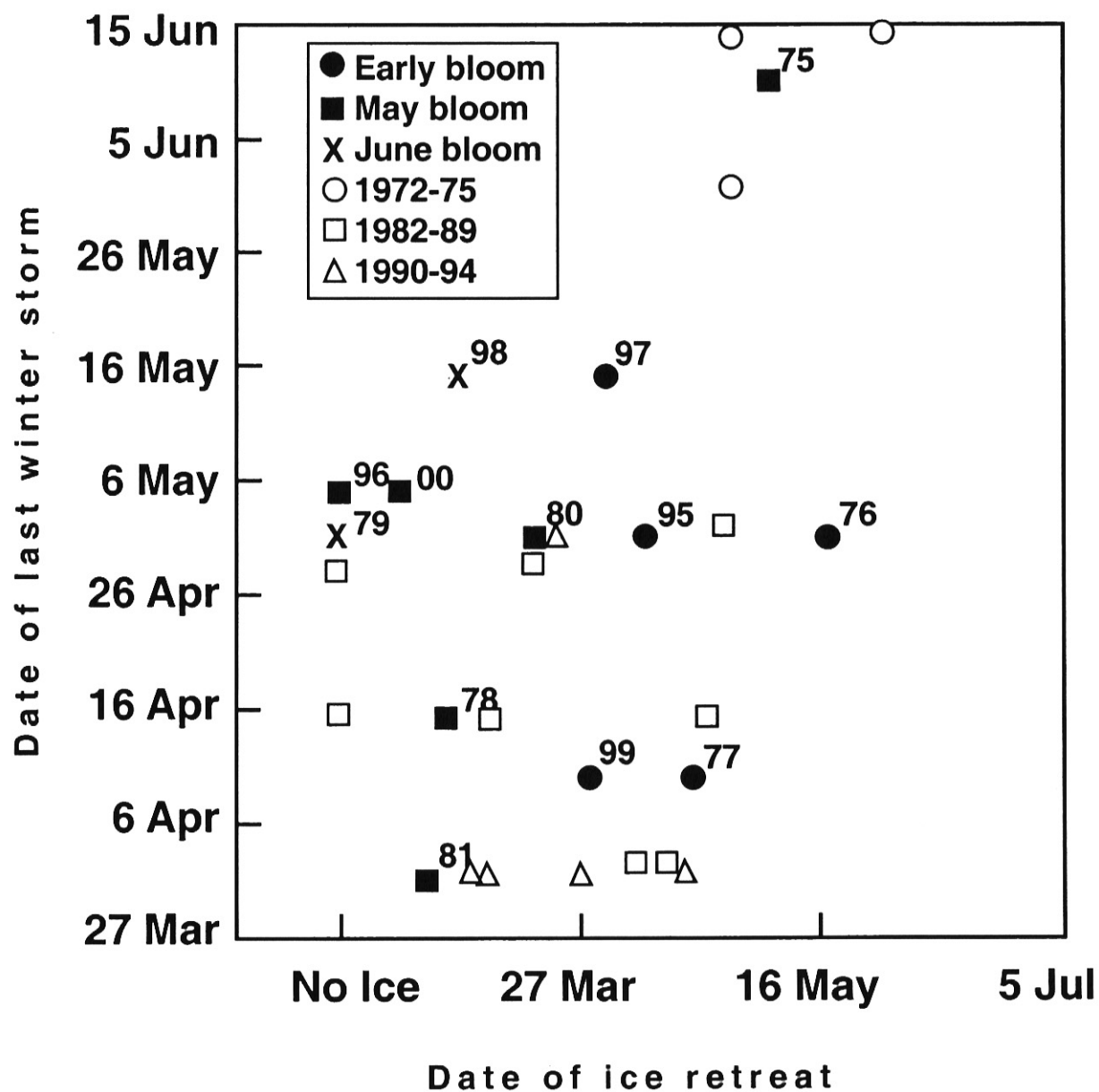
Unit of σ_t Fig. 4



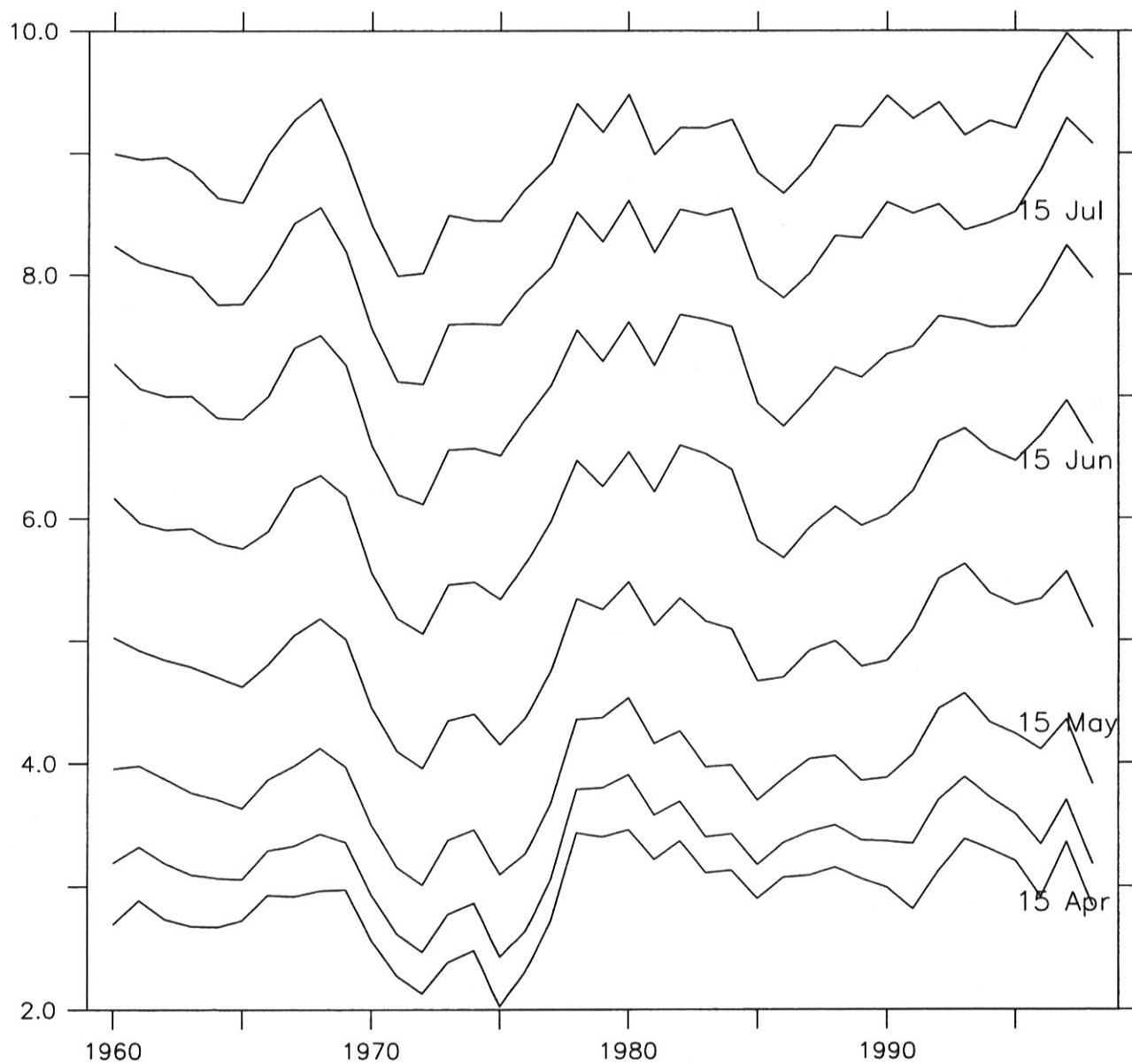
Saint Paul wind speed³

Wind speed

Ice, Mixing and Blooms

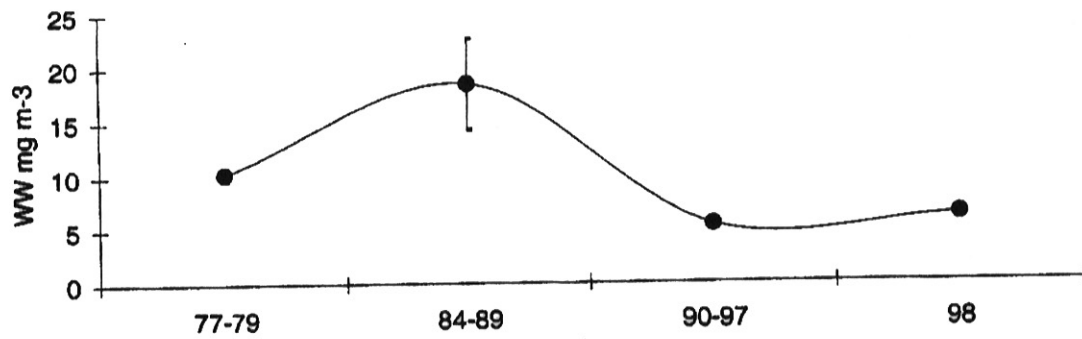


Sea Surface Temperature at 56N, 165W

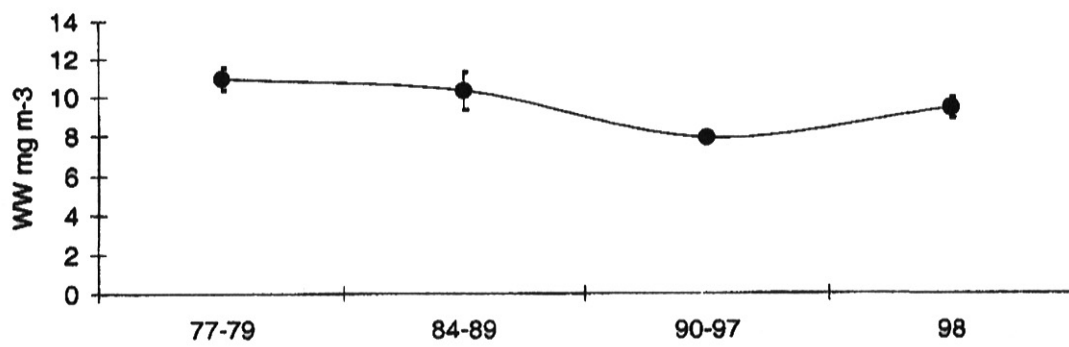


Hunt et al Fig 7

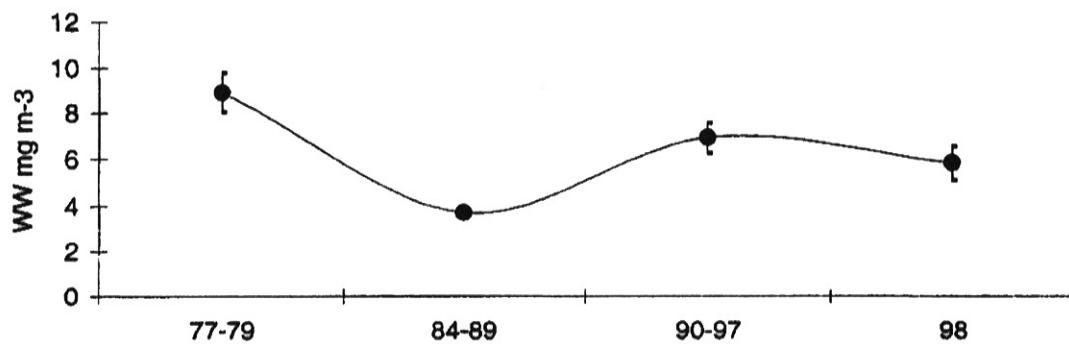
OUTER



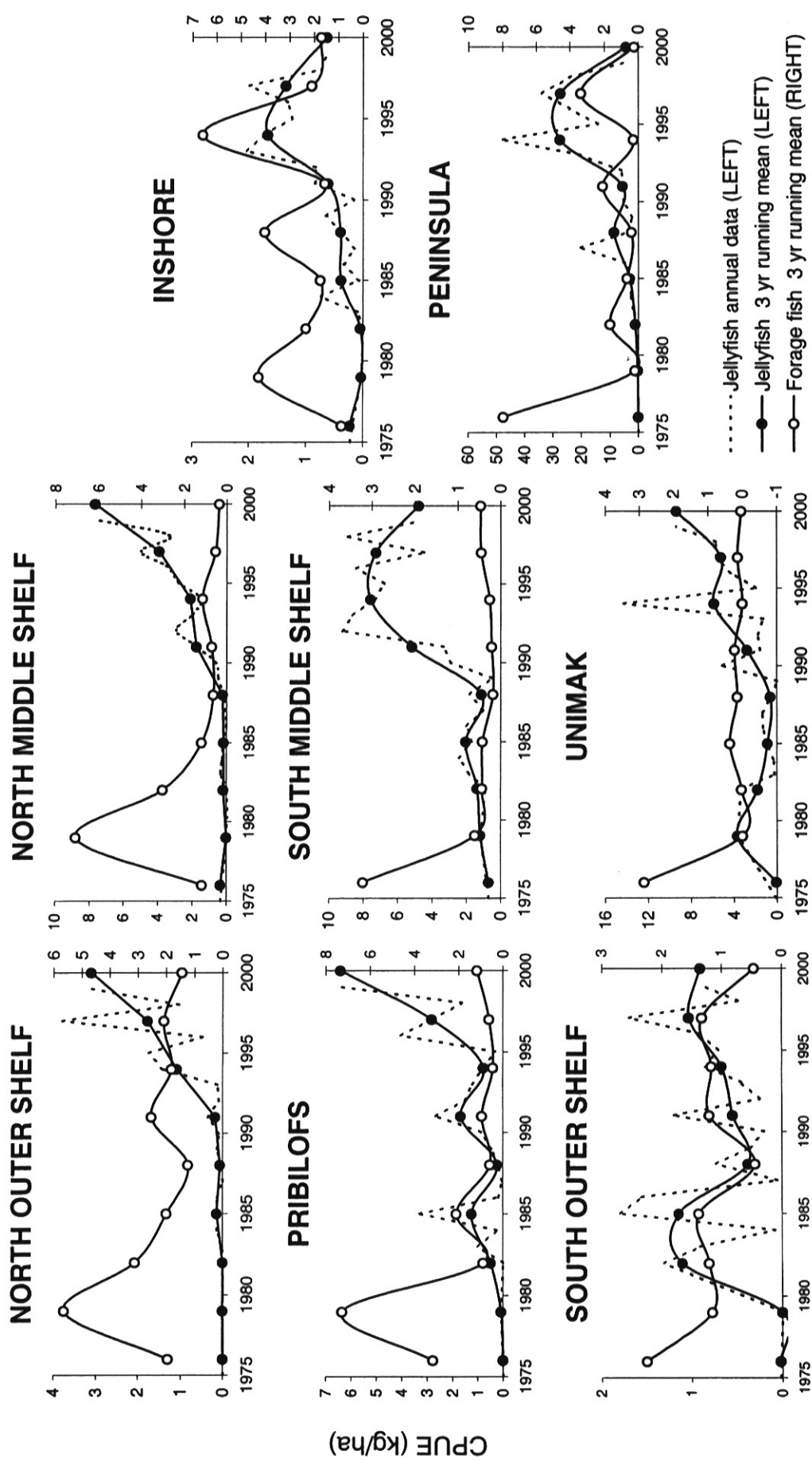
MIDDLE



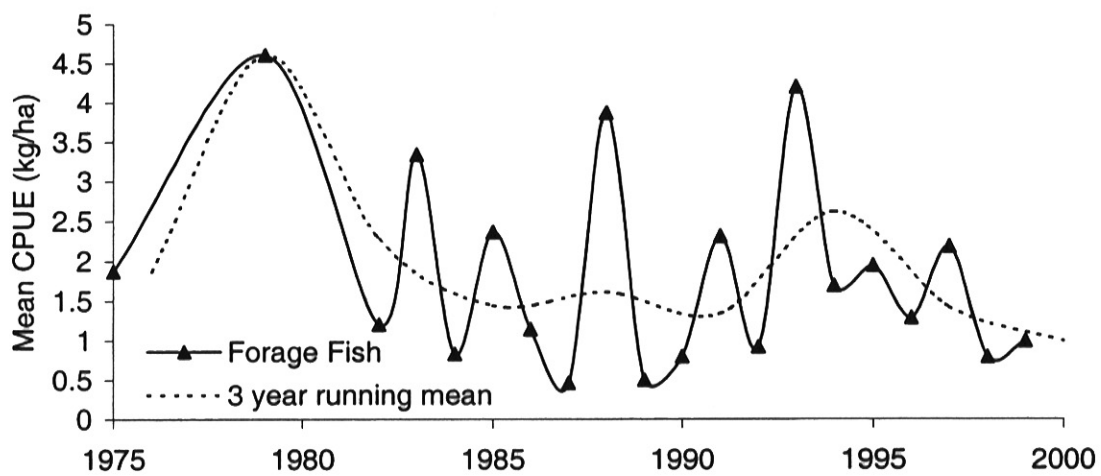
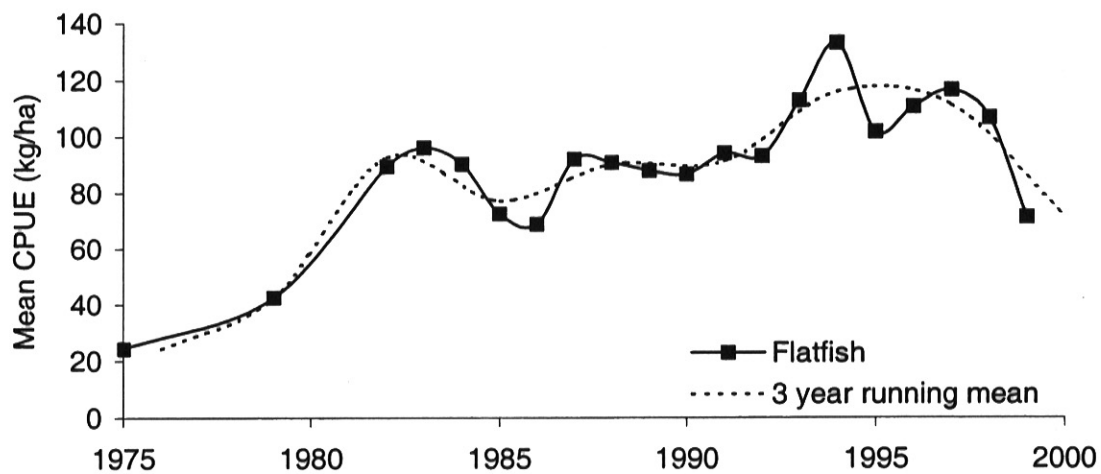
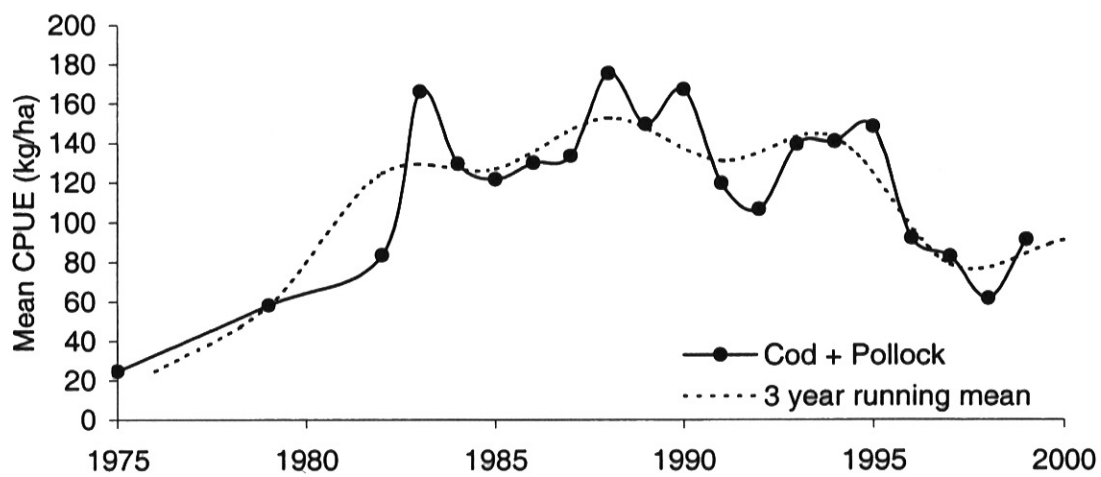
COASTAL

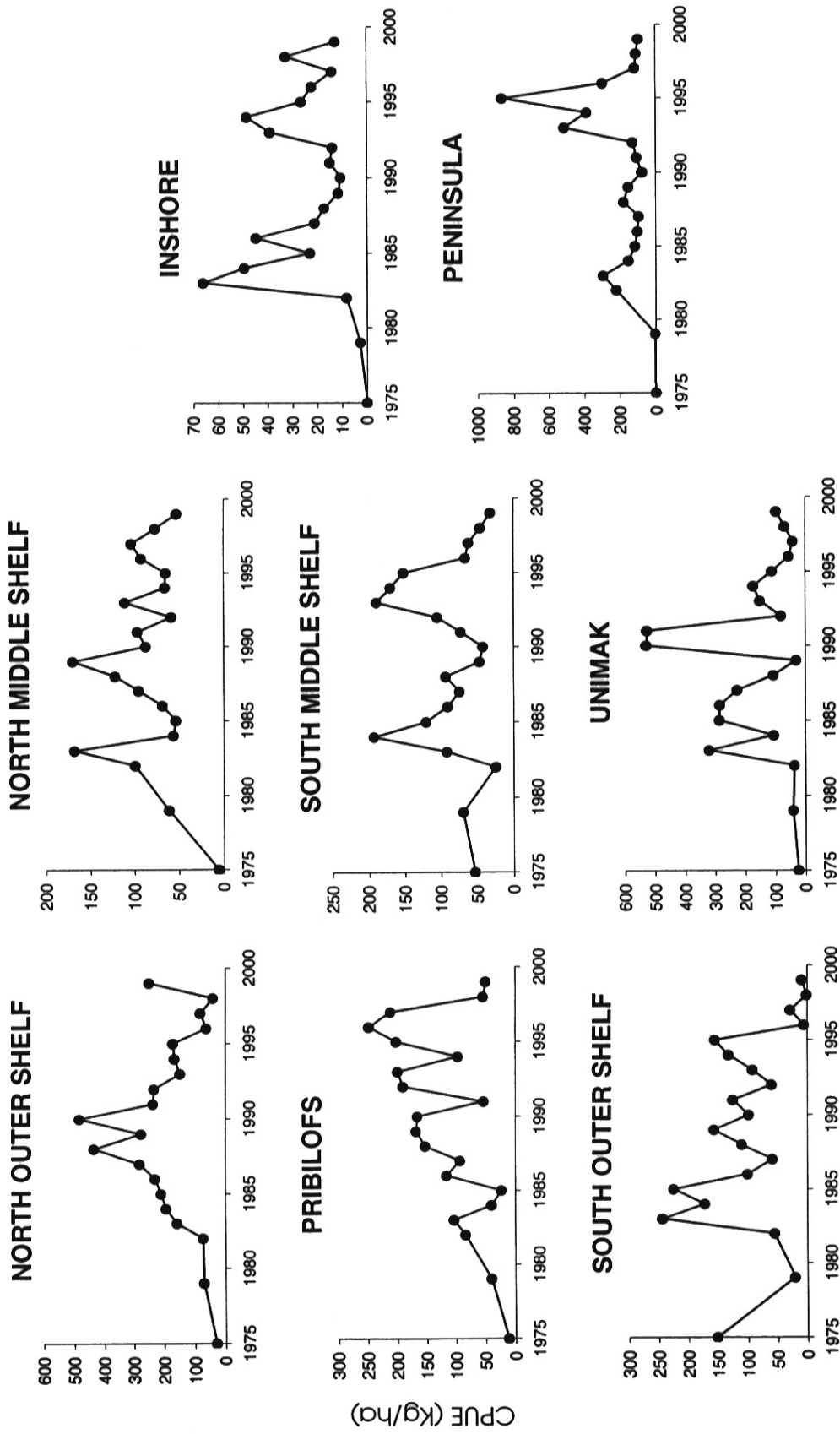


Hunt et al Fig 8

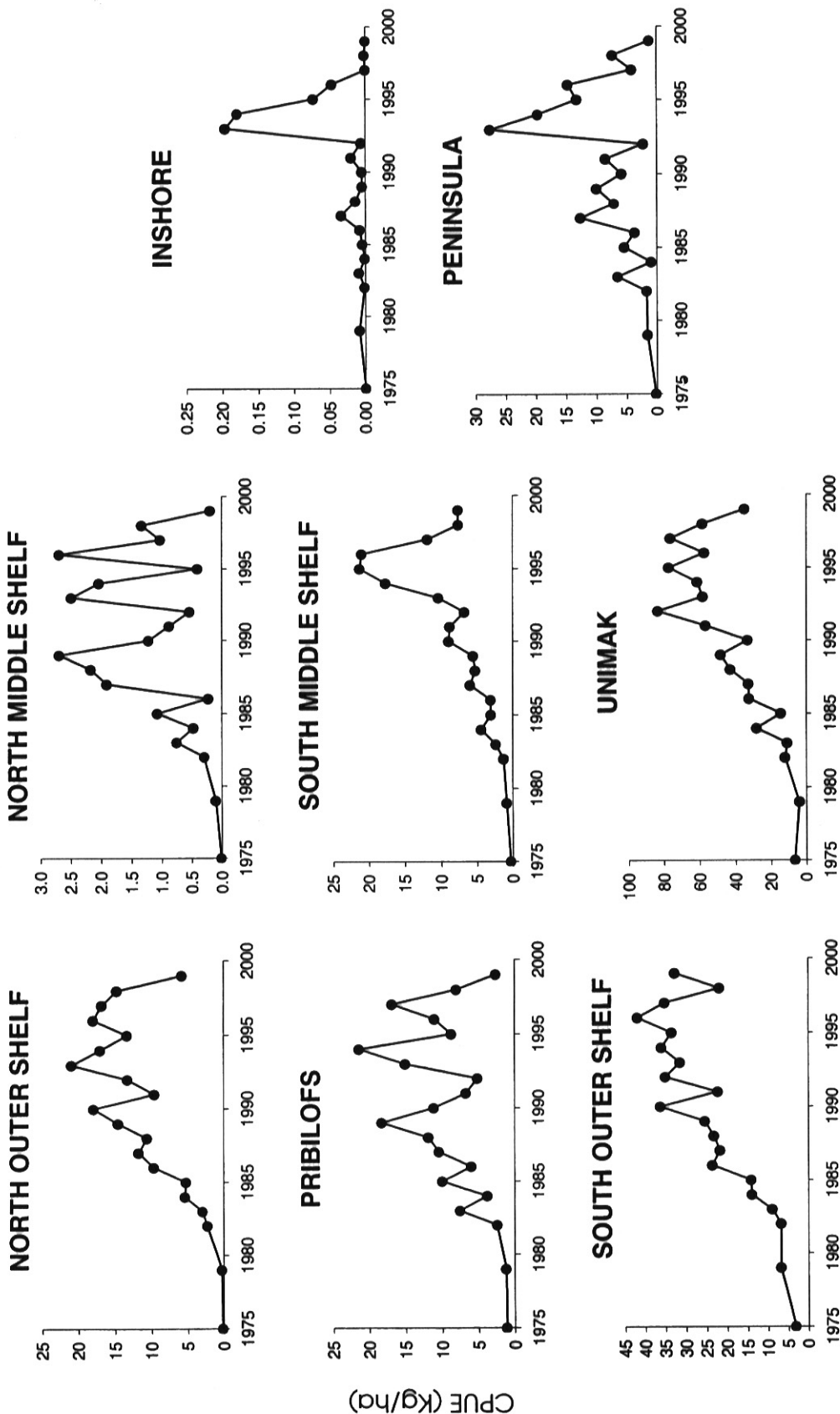


Hand et al. Fig 9

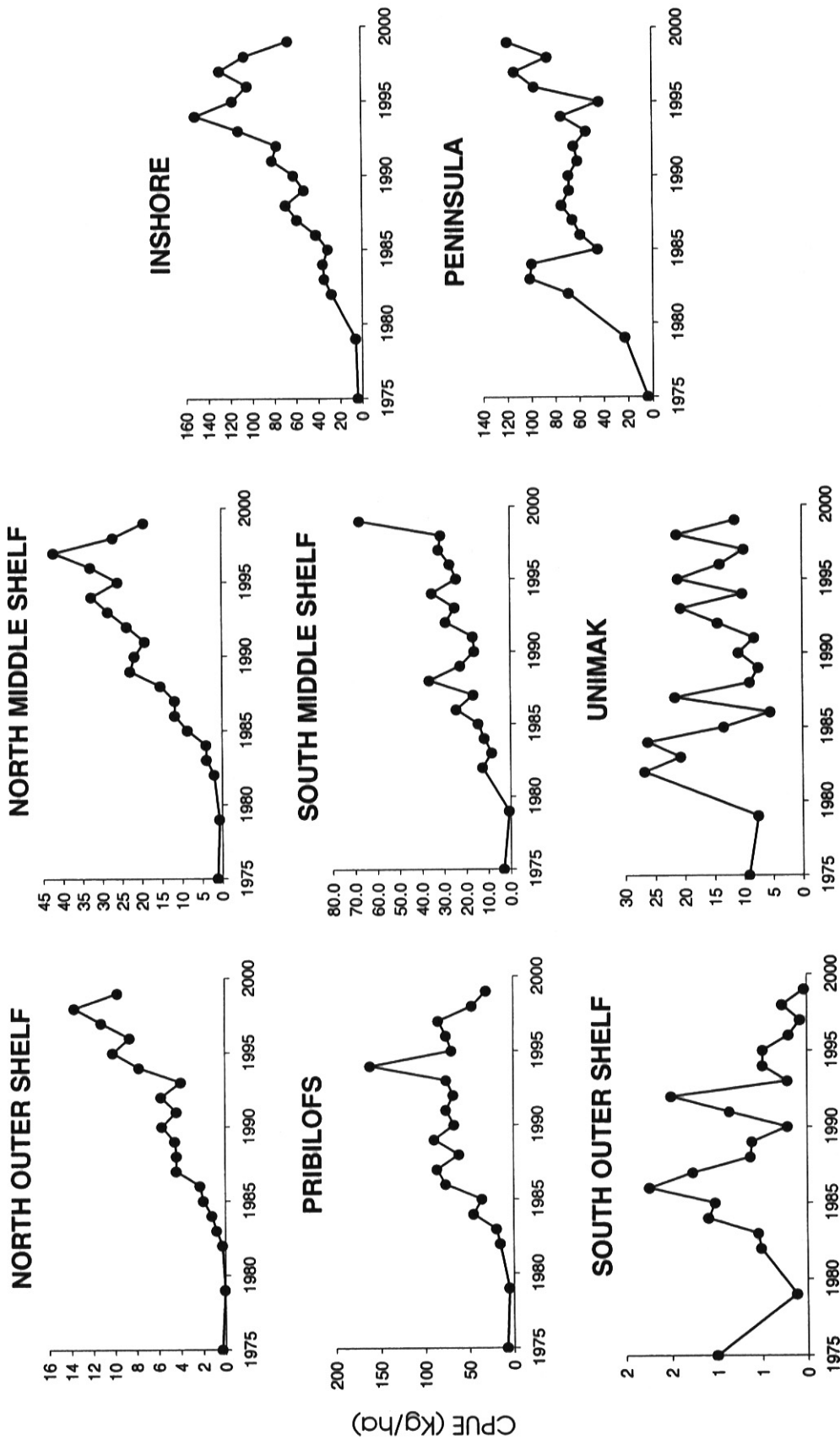




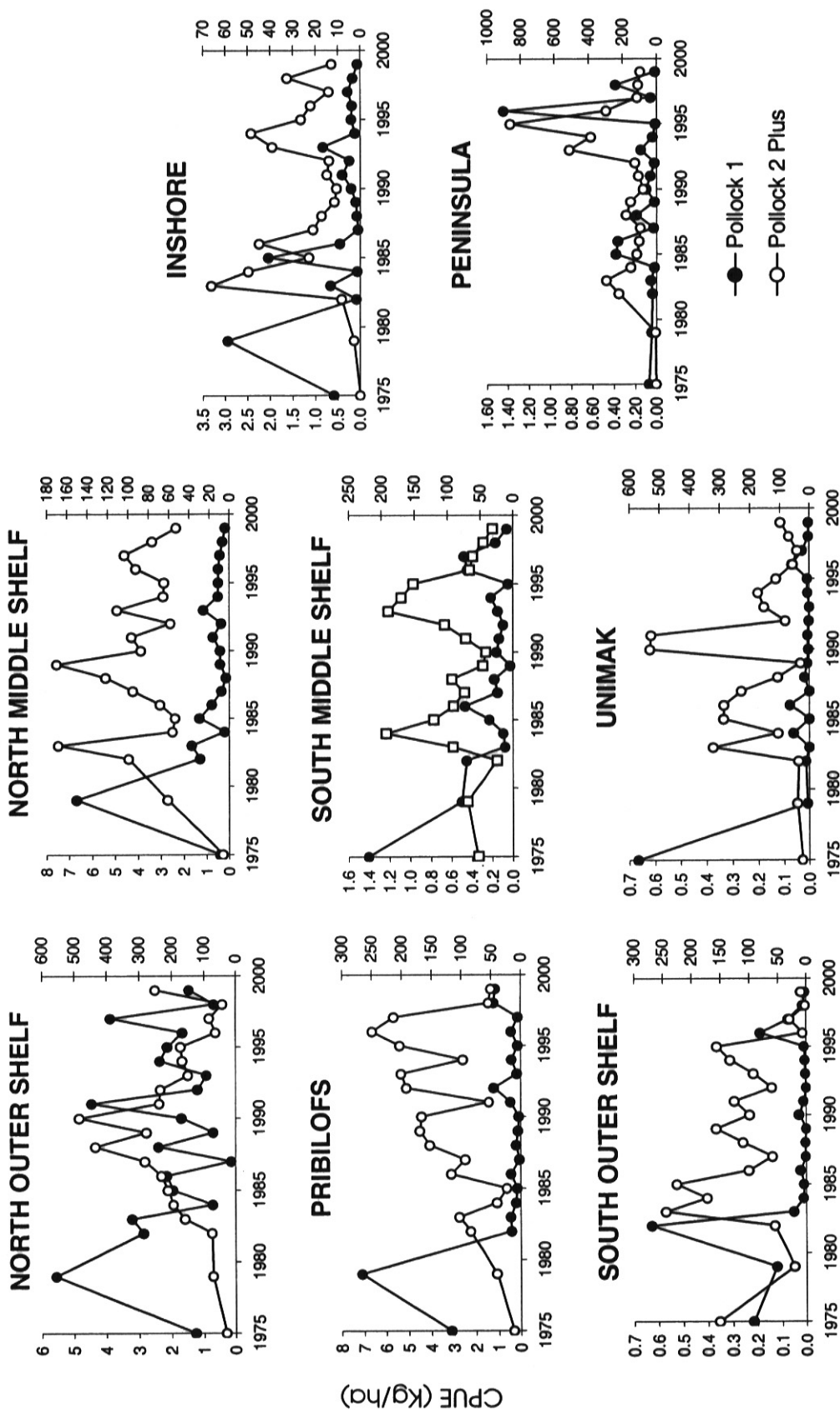
Hunt et al. Fig 11



Hunt et al Fig 12

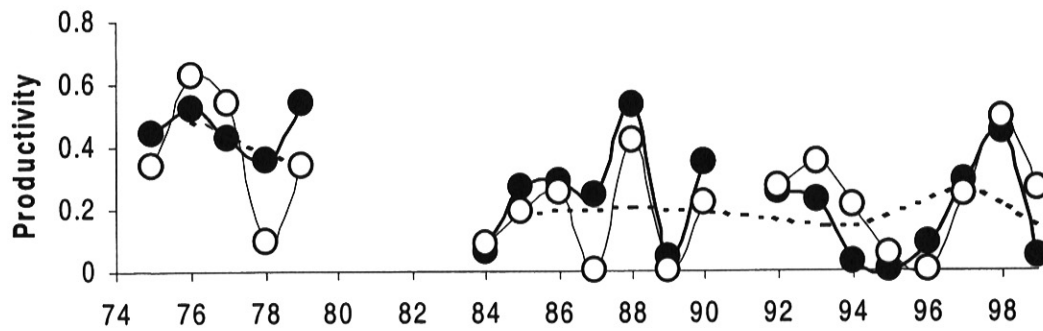


Hunt et al. Fig 13

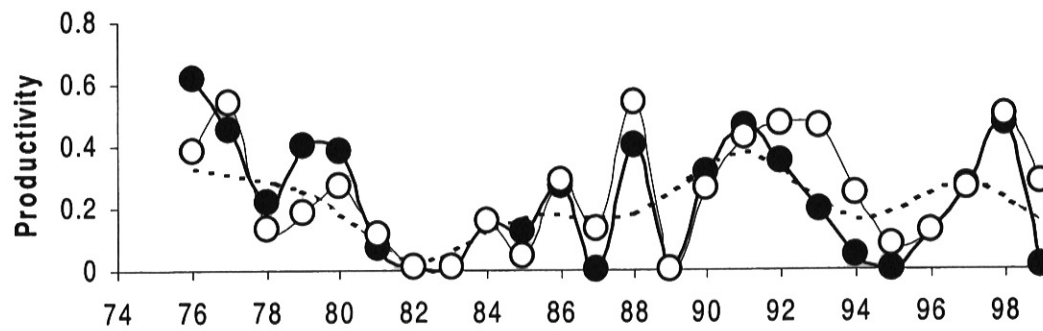


Hunt et. al. Fig. 14

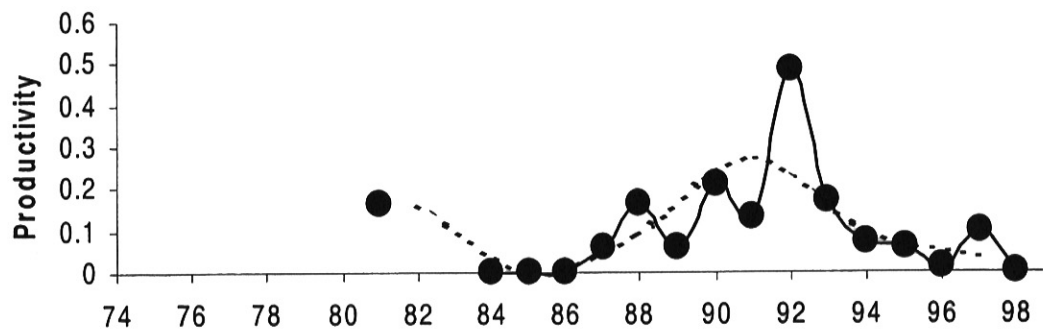
ST. PAUL IS.



ST. GEORGE IS.

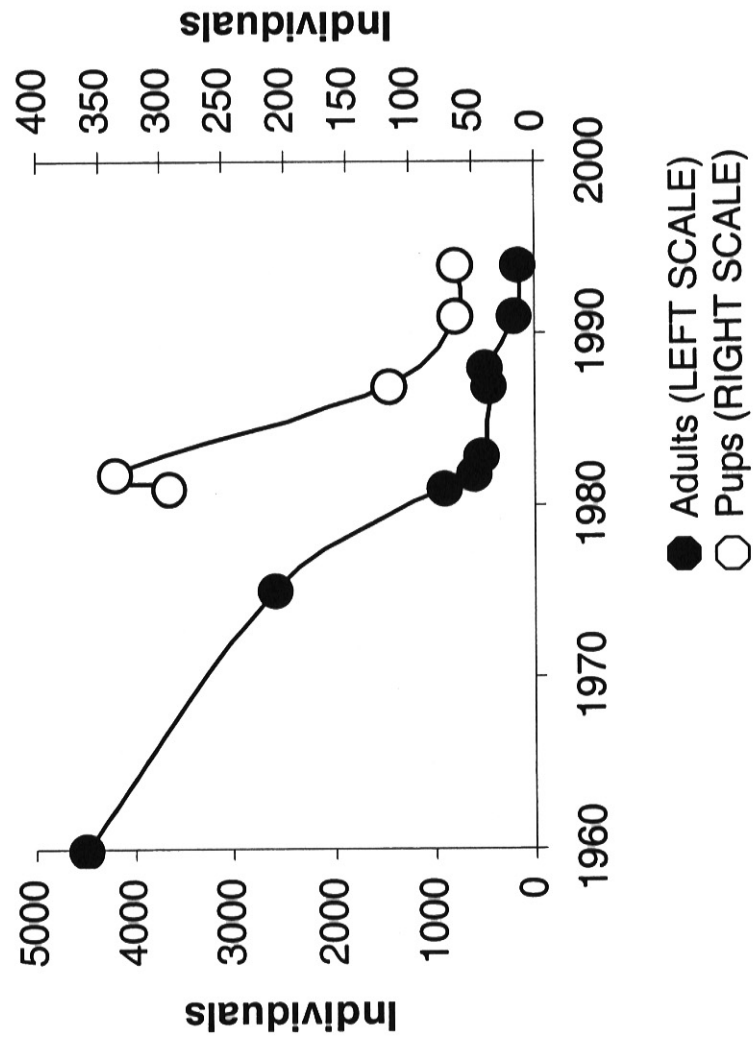


CAPE PEIRCE



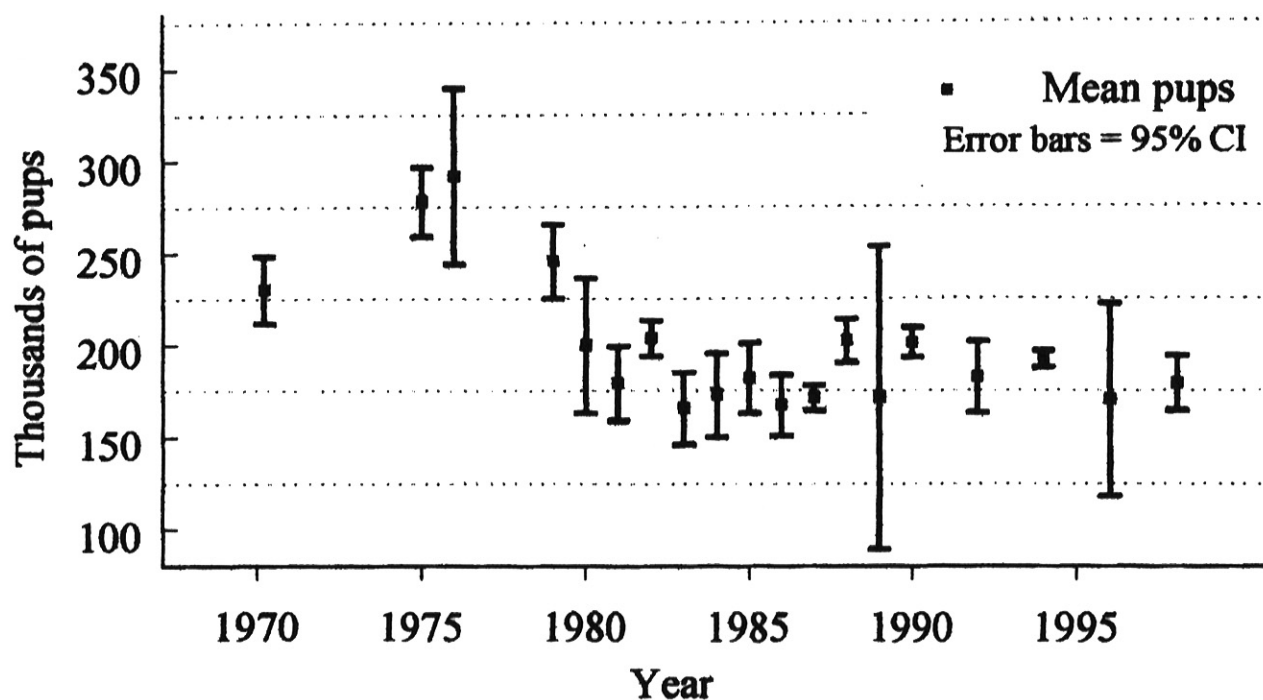
● Black-legged Kittiwake
 ○ Red-legged Kittiwake
 3 year running mean

Hunt et al Fig. 15

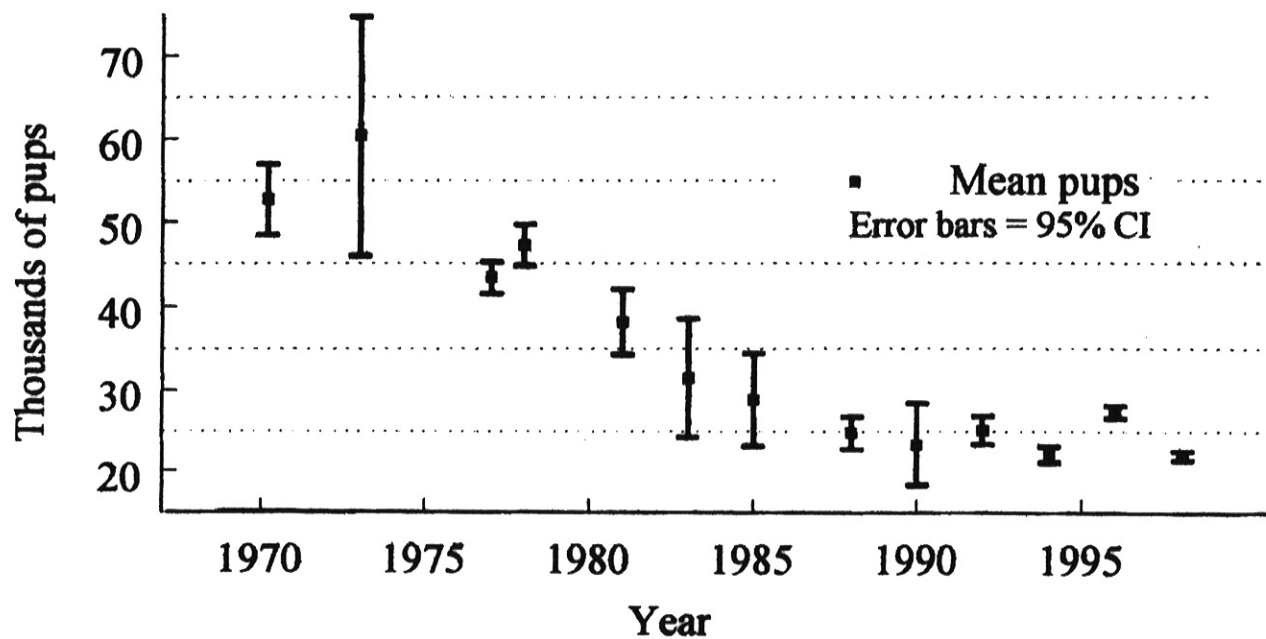


Hunt et al Fig 16

Fur seal pups, St. Paul Island, 1970-98



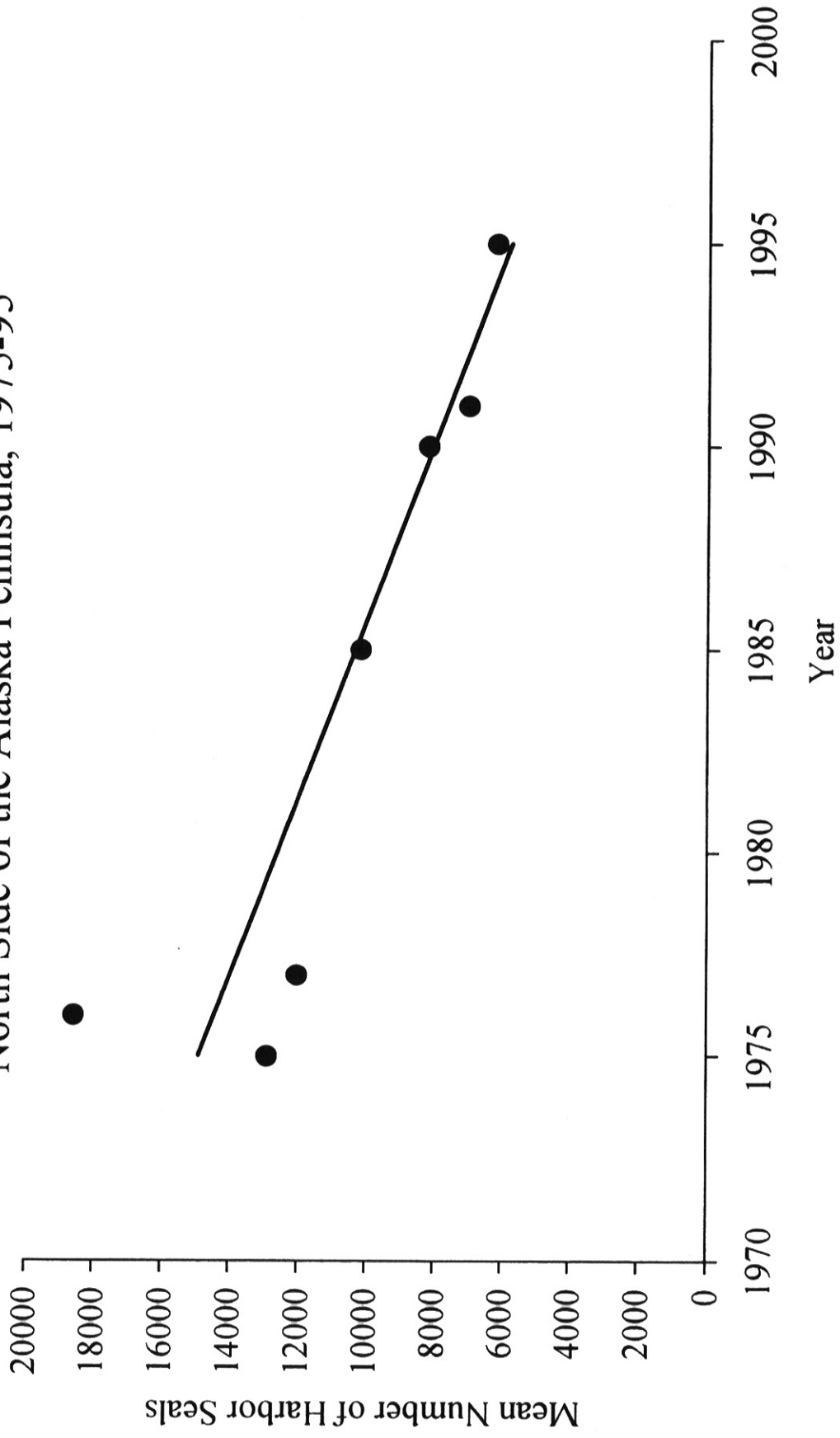
Fur seal pups, St. George Island, 1970-98



Heard et al

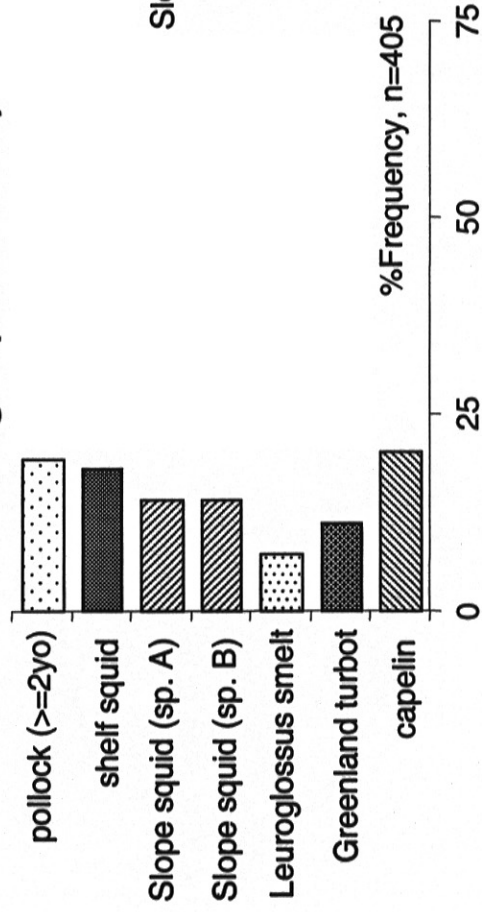
Fig. 17

Regression of Habor Seal Numbers by Year North Side of the Alaska Peninsula, 1975-95

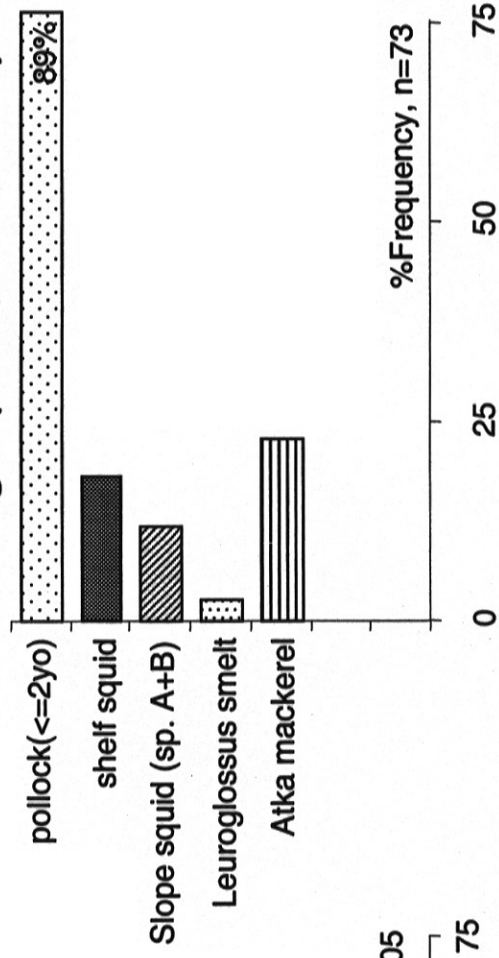


Student of al
Fig 18

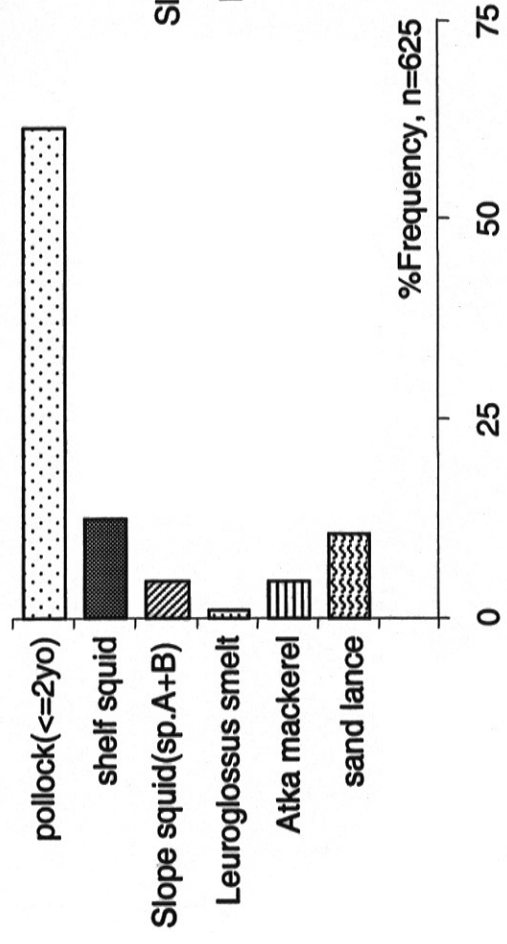
Pelagic (1960-1974)



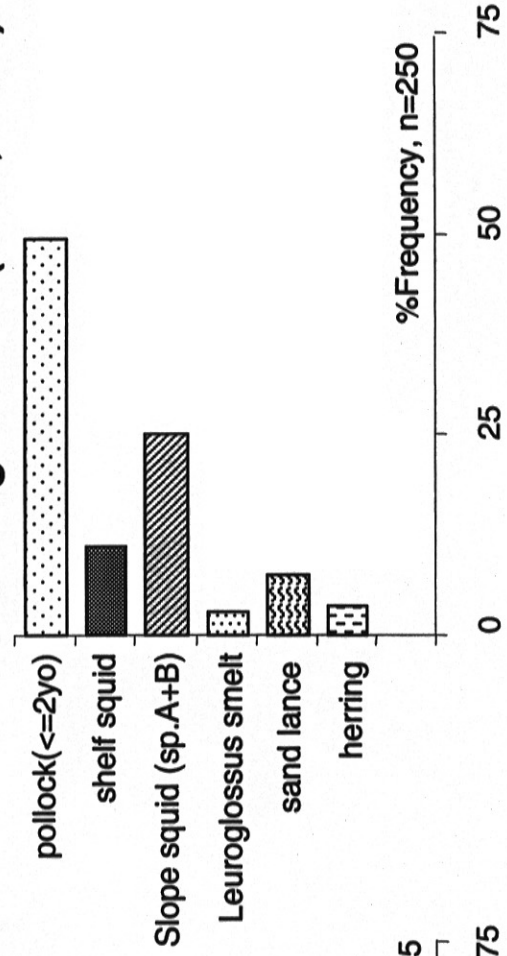
Pelagic (1981, 1982, 1985)



St. Paul Island (1988, 1990)



St. George Island (1988, 1990)



Hunt & Fry 19